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INTRODUCTION TO THE SYMPOSIUM ON SOIL CRUST COMMUNITIES

Larry L. St. Clair[1] and Jeffrey R. Johansen[2]

ABSTRACT—Soil crust communities in semiarid and arid lands around the world have received increasing attention in the past two decades. A symposium on their ecology was presented at the annual meeting of the American Bryological and Lichenological Society held in 1991 in San Antonio, Texas. An introduction to the topic and an overview of the papers appearing in the proceedings volume are given in this prologue.

Key words: cryptogamic crusts, microbiotic crusts, microphytic crusts, semiarid ecosystems, algae crust, lichen crust, moss crust.

In many arid and semiarid regions of the world the surface soil is consolidated into a thin crust by microorganisms, lichens, and bryophytes. Soil crusts have varying microtopography. Some are flattened, polygonal, and possess a rough, undulating surface; others are pediceled. All soil crust communities contain a microflora of cyanobacteria, bacteria, eukaryotic algae, and fungi. Well-developed soil crusts also contain lichens and/or bryophytes.

Soil crusts of biotic origin have been known under a variety of names. Raincrust was one of the first terms used (Fletcher and Martin 1948) but has been abandoned because of confusion with raincrusts of nonbiotic origin. Many researchers designate the crust by its dominant life form, i.e., algal crust, lichen crust, or moss crust. Cryptogamic crust, a term coined by Harper (Kleiner and Harper 1972), has been the most widely used term during the last 20 years. Some researchers have been dissatisfied with the term cryptogamic crust because cryptogams are plants without seeds, a group that includes ferns and fern allies (not components of soil crusts) and excludes cyanobacteria and fungi (not plants). Microfloral crust (Loope and Gifford 1972), microphytic crust (West 1990), microbiotic crust, and cryptobiotic crust (Belnap 1993) are other epithets that have been proposed. Cryptogamic crust will likely persist for some time because of its wide usage and historical precedence. Of the more recent terms, we feel that microbiotic crust is the most accurate and recommend its usage.

Increasing evidence indicates that microbiotic crusts play several vital roles in arid and semiarid rangeland ecosystems. The most important role likely is stabilization of soil surfaces and consequent reduction of soil erosion. Support for this hypothesis has been gathered by several workers (Blackburn 1975, Booth 1941, Fletcher and Martin 1948, Loope and Gifford 1972, MacKenzie and Pearson 1979). In some instances, microbiotic crusts improve seedling establishment by providing moist sites in the cracks and complex topography of the crusts

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[illegible] 1986, St. Clair et al. 1984). Soil [illegible] varying effects on infiltration, and it is unclear whether they improve or worsen water relations in the soil (Harper and Marble 1988, West 1990).

Probably the second most important role microbiotic crusts play is the improvement of soil fertility. Both the free-living and lichenized cyanobacteria fix atmospheric nitrogen in significant amounts (Jeffries et al. 1992, Klubek and Skujins 1980, Rychert et al. 1978, West and Skujins 1977). Furthermore, the crusts contribute to soil organic matter through primary productivity of the cyanobacteria and algae (Jeffries et al. in press). Through contributions of organic material and reduced erosion of silts and clays, cation exchange capacity may be higher in crusted soils.

Microbiotic crusts in North America are most prevalent in the semiarid steppe regions in the Great Basin, Colorado Plateau, and Columbia Basin. They also extend into the hotter, more arid deserts in the southwestern regions of the United States. These regions differ distinctly from semiarid regions east of the Rocky Mountains in that they developed without the pressure of large herds of grazing ungulates (i.e., bison). Antelope, mule deer, and elk grazed the semiarid steppes before the arrival of European settlers, but these herbivores did not graze in large herds and grazed semiarid areas only during the colder months of the year. The dominance of bunchgrasses, shrubs, and microbiotic crust communities in the Intermountain West reflects the historical grazing pressures present in the region (Mack and Thompson 1982).

With the introduction of grazing cattle and sheep, vascular and microbiotic communities have both been impacted. Evidence indicates that domestic grazing animals seriously damage the integrity of the microbiotic crust through trampling of the crust, particularly during dry periods of the year (Anderson, Harper, and Holmgren 1982, Anderson, Harper, and Rushforth 1982, Brotherson et al. 1983, Harper and Marble 1988). Destruction of microbiotic crusts by off-road vehicles and backpackers has [illegible] become a concern in many areas. [illegible] damage microbiotic crust communities [illegible] most of the lichen, moss, and [illegible] Johansen et al. 1982, 1984).

[illegible] development of microb[illegible] by Anderson, Harper, and [illegible] found that silty soils with high electrical conductivity were more likely to develop visible crust features. A few workers have studied recovery of cyanobacteria, lichens, and mosses following disturbance (Anderson, Harper, and Rushforth 1982, Johansen and St. Clair 1986, Johansen et al. 1982, 1984). These studies indicate that algal recovery occurs before lichen and moss recovery, and that the process of full recovery takes many years. St. Clair et al. (1986) demonstrated that recovery can be accelerated through addition of cryptogamic amendments. Despite these studies, our current understanding of recovery of microbiotic crusts is very limited.

Microbiotic soil crusts of arid and semiarid rangelands have received considerable attention in the literature. They have been the subject of no fewer than six reviews in the past four years (Dunne 1989, Harper and Marble 1988, Isichei 1990, Johansen 1993, Metting 1991, West 1990). In the past 50 years over one hundred papers have been published on various aspects of the composition, distribution, physical properties, and ecology of arid/semiarid soil crusts. There is a growing consensus among researchers that these crusts play an important beneficial role in the ecosystems in which they occur. However, unanimity does not exist. In particular, West (Gutknecht 1991, West 1990) has questioned the ecological value of microbiotic crusts and called for more rigorous studies of their ecology, physical properties, and response to disturbance.

Because of the interest in microbiotic crust communities and the current debate over their role in semiarid and arid ecosystems, a symposium on soil crust communities was held at the annual meeting of the American Bryological and Lichenological Society in San Antonio, Texas, 5 August 1991. This issue of the *Great Basin Naturalist* contains the proceedings of that symposium as well as other related papers on microbiotic soil crusts.

The first part of the volume contains various papers dealing with floristics and distribution of various crust components. St. Clair et al. (1993) review the distribution of soil lichens in the arid and semiarid regions of the Intermountain West of the United States, and address the impact of disturbance on soil lichen communities in this region. A report on the bryophytes of calcareous soils of a semiarid region of south central Australia is given by Downing and Selkirk (1993). Grondin and Johansen (1993) give a preliminary species list of soil algae from Colorado National Monument and discuss the spatial heterogeneity of cyanobacteria and coccoid eukaryotic algae in crusts of the monument. Wheeler et al. (1993), in a companion paper to the work by Grondin and Johansen (1993), report on the spatial heterogeneity of bacterial populations in microbiotic crusts. Finally, Belnap and Gardner (1993) present an electron microscopical study of *Microcoleus vaginatus* (Vauch.) Gomont, which elucidates the role that *Microcoleus* plays in the microstructure of microbiotic crusts.

The second part of the volume addresses the ecology of the microbiotic crusts. Our understanding of the relationship between microbiotic crusts and soil hydrology is furthered in a study of semiarid woodlands of Australia by Eldridge (1993). Contributions of microbiotic crusts to soil fertility are discussed by Harper and Pendleton (1993), who present data indicating that cyanobacteria and cyanobacterial lichens may enhance the availability of several essential minerals for higher plants. Johansen et al. (1993) present the results of a study of the impact of rangefire on soil algal communities in the Columbia Basin and the degree of recovery during the two years following fire. In the final paper, Belnap (1993) discusses the use of inoculants in speeding recovery of microbiotic crusts.

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LICHENS OF SOIL CRUST COMMUNITIES IN THE INTERMOUNTAIN AREA OF THE WESTERN UNITED STATES

Larry L. St. Clair[1,2], Jeffrey R. Johansen[3], and Samuel R. Rushforth[1]

ABSTRACT—Lichens are common components of microbiotic soil crusts. A total of 34 species from 17 genera are reported from soil crust communities throughout the Intermountain Area. Distribution of terricolous lichens is determined by various physical and biological factors: physical and chemical characteristics of the soil, moisture regimes, temperature, insolation, and development and composition of the vascular plant community. Some species demonstrate a broad ecological amplitude while others have a more restricted distribution. All growth forms are represented; however, the vast majority of soil crust lichens are squamulose (minutely foliose). Fruticose species are least abundant. In exposed, middle-elevation sites vagrant (detached) species are common. This paper describes and discusses terricolous lichen communities of desert habitats of the intermountain western United States. Effects of various human-related activities including grazing, wildfire, air pollution, and recreation vehicles on soil crust lichens are discussed. *Gypsoplaca macrophylla* (Zahlbr.) Timdal, a rare squamulose lichen which occurs on gypsiferous soils, was recently collected in Emery County, Utah, and is reported as new to the state.

Key words: lichens, cryptogamic crusts, microbiotic crusts.

Lichens are common components of soil crust communities. In some habitats lichens account for a significant percentage of the ground cover, often stabilizing the soil surface and enhancing soil fertility. Over the last 25 years extensive studies have been undertaken in arid and semiarid western North America in an effort to better understand the ecological role of microbiotic soil crusts. Initial studies described various biological components (Anderson and Rushforth 1976, Johansen et al. 1981). Other studies considered various ecological aspects of soil crust communities (Anderson, Harper, and Holmgren 1982, Brotherson and Rushforth 1983, Kleiner and Harper 1977, St. Clair et al. 1984, Skujins and Klubek 1978). Human-induced damage to soil crust communites has also been studied (Johansen et al. 1984, Johansen and St. Clair 1986). Some research has investigated recovery and reclamation/restoration of damaged soil crust communities (Anderson, Harper, and Rushforth 1982, St. Clair et al. 1986).

Several lichen floras and checklists for the Intermountain Area have been published (Egan 1972, Nash and Johnsen 1975, Newberry 1991, St. Clair and Newberry 1991, Schroeder et al. 1975, Shushan and Anderson 1969). However, very few studies have dealt directly with soil lichens. Anderson and Rushforth (1976) published the only list of lichens from desert soils in the Intermountain West. They collected lichens from 34 sites in three distinct areas of southern Utah. Most of the sites (27) were located in the Great Basin. Five were in gypsiferous habitats in Washington County, while the remaining sites were located in pristine, open grassy areas in Canyonlands National Park. They reported a total of 17 species in 11 genera; however, 3 of the species were saxicolous and 6 of the remaining species were misidentified. Nash and Sigal (1981) published a checklist of the lichens of Zion National Park in connection with a preliminary air-quality survey for the park. They reported a total of 159 species in 53 genera from their collections. Nine of the species were terricolous lichens from middle-elevation desert habitats. Two recent monographic works (Thomson 1987, 1989, Timdal 1986) have added significant taxonomic and ecological information about two of the more abundant soil genera in western North America (*Psora* and *Catapyrenium*). St. Clair and

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Weber (1986) reported *Acarospora nodulosa* (Duf.) Hue var. *nodulosa*, a squamulose soil lichen collected from gypsiferous soils in southern Utah, as a new record for North America. Timdal (1990) described a new and rare squamiform lichen genus and family (*Gypsoplaca* of the Gypsoplacaceae) from gypsiferous soils in southwestern Colorado. Timdal included with his description a list of 21 soil crust species commonly associated with *Gypsoplaca macrophylla*. Many species on Timdal's list are commonly found on gypsiferous soils throughout the Colorado Plateau. Recently, Newberry (1991) characterized the lichen flora of the Uinta Mountains of northeastern Utah, listing a total of 291 taxa in 95 genera from his collections. As part of his study he made extensive collections of soil crust lichens along the northern border of the Colorado Plateau. Rosentreter and McCune (1992) described distribution patterns of vagrant species of the foliose genus *Dermatocarpon* in Idaho, Montana, Wyoming, and eastern Oregon and Washington.

The purpose of this paper is to characterize the lichen component of desert soil crust communities in intermountain western North America. This paper is based on a careful review of the literature as well as unpublished observations and collections made by the authors and others throughout the Intermountain Area over the last 14 years.

Results and Discussion

Soil Crust Community Structure

Most soil crust lichens are either squamulose or foliose (79%). Squamulose (minutely foliose) species are particularly common. Of the 34 species currently known from soil crust communities in the Intermountain Area, 59% are squamulose, 21% foliose, 12% crustose, and 9% fruticose (Table 1). Of the 20 squamulose species, 9 are in the genus *Psora*.

All fruticose and most foliose species are vagrant (unattached), the only exceptions being *Xanthoparmelia wyomingica*, which is loosely adnate over rocky soils, and *X. idahoensis*, which is often loosely attached to the soil surface. All vagrant forms tend to become entangled either with vascular plants or with detritus, and during wet periods they may even become temporarily attached. Rogers (1977) suggested that many vagrant forms are simply detached [illegible] normally attached species." Careful evaluation of the vagrant lichens of the Intermountain Area shows that Rogers's conclusion is probably accurate for at least some species. For example, *Rhizoplaca haydenii* is commonly collected from habitats in which adjacent rocks are covered with the attached, umbilicate lichen *R. melanophthalma*. This situation has led some lichenologists to seriously question whether *R. haydenii* is simply a detached form of *R. melanophthalma*. Rosentreter and McCune (1992) have also reviewed the status of the vagrant lichen *Dermatocarpon vagans*. After carefully comparing *D. vagans* with *D. reticulatum* and *D. miniatum*, they concluded that the vagrant form is simply detached fragments of *D. reticulatum* and *D. miniatum*. Similar discussions have taken place concerning *Agrestia hispida*, with some lichenologists (Weber 1967) suggesting that *A. hispida* is simply an environmental modification of the attached crustose lichen *Aspicilia calcarea*. The only exception to this general pattern may be *Xanthoparmelia chlorochroa*, which at least in some habitats seems to be a true vagrant with no local attached members. However, in other habitats vagrant specimens of *X. chlorochroa* occur sympatrically with several species of *Xanthoparmelia* that grow over rocks and onto the soil. The issue is somewhat confusing; however, Rogers's conclusion is probably correct, at least in some cases.

Squamulose and crustose lichens dominate open Great Basin sites with vagrant forms conspicuously absent. The three most common lichen species from the Great Basin are *Collema tenax*, *Catapyrenium lachneum*, and *Caloplaca tominii* (Table 1). Development and distribution of soil crust communities in the Great Basin seem to be correlated with the occurrence of vascular plants. Intershrub spaces are dominated by cyanobacterial and lichen crusts while the area immediately beneath shrubs is dominated by various moss and vascular species. A combination of several factors, including moisture, insolation, and perhaps even allelopathic activity (Schlatterer and Tisdale 1969), seems to be dictating this pattern.

Gypsiferous soils have the best developed lichen communities, often with 100% lichen cover. Species diversity is also very high at gypsiferous sites, with several rare species (e.g., *Acarospora nodulosa* var. *nodulosa* and *Gypsoplaca macrophylla*) becoming common to abundant. The most abundant species on

TABLE 1. Distribution of terricolous lichen species from the Intermountain Region of western United States. Growth form: Cr = crustose, Fo = foliose, Fr = fruticose, Sq = squamulose. Habit: A = attached, V = vagrant. Relative abundance: A = abundant, C = common, R = rare.

			Intermountain Area soil lichen habitats			
Species	Growth form	Habit	Great Basin	Gypsiferous	Steppe	Upland
Acarospora nodulosa (Dufour) Hue	Sq	A		C-A		
Acarospora nodulosa var. *reagens* Zahlbr.) Clauz. & Roux	Sq	A		R-C		
Agrestia hispida (Mereschk.) Hale & Culb.	Fr	V			C-A	R-C
Aspicilia reptans (Looman) Wetm.	Fr	V			R	
Aspicilia sp.	Fr	V			C-A	
Buellia elegans Poelt	Sq	A	R-C	C-A		R
Caloplaca tominii Saviez	Cr	A	C			R
Catapyrenium daedaleum (Krempelh.) B. Stein	Sq	A				R
Catapyrenium lachneum (Ach.) R. Sant.	Sq	A	C-A	C-A	C	C
Collema tenax (Swartz) Ach.	Sq	A	C-A	C	R-C	R-C
Dermatocarpon miniatum (L.) Mann	Fo	V			R-C	
Dermatocarpon reticulatum Magn.	Fo	V			R-C	
Diploschistes diacapsis (Ach.) Lumbsch	Cr	A	A			
Endocarpon pusillum Hedwig	Sq	A	R			R
Fulgensia desertorum (Tomin) Poelt	Cr	A		C		
Fulgensia fulgens (Swartz) Elenkin	Sq	A	R-C			R-C
Gypsoplaca macrophylla (Zahlbr.) Timdal	Sq	A		R-C		
Psora cerebriformis W. Weber	Sq	A	R-C			C-A
Psora crenata (Taylor) Reinke	Sq	A		C		
Psora decipiens (Hedwig.) Hoffm.	Sq	A	C-A	C	C	C
Psora globifera (Ach.) Massal.	Sq	A	R			
Psora icterica (Mont.) Muell.	Sq	A				C
Psora luridella (Tuck.) Fink	Sq	A	R			
Psora montana Timdal	Sq	A				R
Psora russellii (Tuck.) A. Schneider	Sq	A				R
Psora tuckermanii R. Anderson ex Timdal	Sq	A	C-A			C
Rhizoplaca haydenii (Tuck.) W. Weber	Fo	V			C-A	
Squamarina lentigera (Weber) Poelt	Sq	A		C-A		R
Toninia caeruleonigricans (Lightf.) Th. Fr.	Cr	A	R-C	R-C		R
Toninia tristis (Th. Fr.) Th. Fr.	Sq	A				R
Xanthoparmelia chlorochroa (Tuck.) Hale	Fo	V			C-A	R-C
Xanthoparmelia idahoensis Hale	Fo	A V				R-C
Xanthoparmelia lipchlorochroa Hale & Elix	Fo	V			C-A	
Xanthoparmelia wyomingica (Gyelnik) Hale	Fo	V			C-A	

gypsiferous soils are *Diploschistes diacapsis* and *Squamarina lentigera* (Table 1). Vagrant species are also missing from gypsiferous sites.

Upland, sandy sites in pinyon-juniper woodlands are dominated by various species of the genus *Psora*, including *P. cerebriformis*, *P. tuckermanii*, and *P. decipiens*. *Catapyrenium lachneum* and *Endocarpon pusillum* are also found at these sites (Table 1). Vagrant species are present but rare in upland sites. *Xanthoparmelia chlorochroa* and *Agrestia hispida* have been collected from this habitat type.

Dry, upland steppe sites dominated by various *Artemisia* spp. often have well-developed vagrant lichen floras including *Xanthoparmelia chlorochroa*, *Rhizoplaca haydenii*, *Dermatocarpon reticulatum*, and *Agrestia hispida*. The squamulose species *Catapyrenium lachneum* and *Collema coccophorum*, also commonly found in this type of habitat (Table 1).

Some species of soil crust lichens are both broadly distributed and generally abundant, occurring throughout the full range of soil crust habitats in the Intermountain Area. For example, the squamulose lichens *Psora decipiens* and *Catapyrenium lachneum* are common components of all desert habitats in the Intermountain Area, occurring on calcareous, gypsiferous, and sandy upland soils. They are also common components of alpine tundra habitats throughout intermountain North America. Both species have also been collected worldwide from Australia, Africa, Asia, and Europe (Rogers and Lange 1972). Other species are broadly distributed but are much less abundant. Such taxa include *Endocarpon pusillum*, *Toninia caeruleonigricans*, and *Buellia elegans*. Gelatinous lichens (e.g., *Collema* sp. and *Peccania* sp.) are abundant but not particularly well known from western soil crust communities. More careful analysis of this group, particularly on gypsiferous soils, will invariably yield several additional species. Presently, the taxon *Collema tenax* is probably overused.

One group of lichens conspicuously missing from the intermountain deserts is the genus *Cladonia*. Although this genus occurs commonly on the Great Plains, in the boreal forest, and on the alpine tundra, it is not represented by a single species in the soil crust communities of the Great Basin or Colorado Plateau.

Affinities of Intermountain Area Soil Crust Lichens

Very little descriptive or ecological information is available for the lichen component of soil crust communities in the Intermountain Area. Looman (1964), whose work was the first to specifically characterize terricolous lichen communities in North America, focused on the Prairie Provinces of Canada and adjacent parts of the northern Great Plains. He specifically described the Parmelietum chlorochroae lichen association, a steppe community with arctic-alpine affinities. Floristically, this association is very similar to the lichen soil crust communities of the Intermountain Area. This association includes several common species (e.g., *Xanthoparmelia chlorochroa*, [illegible] *Rhizoplaca haydenii*, and *Aspicilia* [illegible]) that are also common components of the short-grass–shrubland steppe of western Wyoming, Idaho, eastern Montana, northwestern Utah, and northeastern Colorado. Other species included in this association, namely *Catapyrenium lachneum*, *Endocarpon pusillum*, *Collema tenax*, *Psora decipiens*, *Toninia caeruleonigricans*, *Fulgensia fulgens*, *Buellia elegans*, and *Squamarina lentigera*, also occur in the Intermountain Area. Some species occur in both the Great Basin and the Colorado Plateau, while others are limited to one or the other. Other taxa included in Looman's Parmelietum chlorochroae association (e.g., *Cladonia pocillum*, *Phaeorrhiza nimbosa*, and *Acarospora schleicheri*) are absent from the middle-elevation deserts of the Intermountain Area but are commonly found in intermountain boreal and/or alpine tundra habitats.

European lichenologists have described two lichen associations, Fulgensietum fulgentis and Parmelietum vagantis, which are very similar to the soil lichen communities of the Great Basin and Colorado Plateau (Klement 1955, 1958). The combined species list for the two European associations is virtually identical to Looman's Parmelietum chlorochroae association list. Floristically, the Fulgensietum fulgentis association is more closely related to the Great Basin and Colorado Plateau soil lichen communities, while Parmelietum vagantis more closely resembles the short-grass–shrubland steppe community of western Wyoming, Idaho, eastern Montana, northeastern Utah, and northwestern Colorado. The Intermountain Area seems to have four distinctive soil lichen associations (Table 1): calcareous Great Basin soil crusts, sandy Colorado Plateau soil crusts, gypsiferous soil crusts, and northern steppe soil crusts. Some species are found in all four associations, while other species are unique to a given association (Table 1).

Annotated List of Soil Crust Taxa

***Acarospora nodulosa* (Dufour) Hue var. *nodulosa*.** A squamulose species locally abundant on gypsiferous soils. This species was reported new to North America by St. Clair and Warrick in 1987. Original collections of this species were made in Washington County, Utah, with subsequent collections from similar habitats in Emery County, Utah, and northwestern Arizona.

***Acarospora nodulosa* (Dufour) Hue var. *reagens*.** A squamulose lichen collected from Montrose and San Miguel counties in southwestern Colorado. Locally common on gypsiferous soils. This species has not been collected in Utah; however, more careful examination of gypsiferous soil habitats in the state will likely confirm its occurrence in Utah and perhaps even the northwestern corner of Arizona.

***Agrestia hispida* (Mereschk.) Hale & Culb.** A fruticose, vagrant lichen that demonstrates tremendous morphological plasticity. This species is part of a complicated group of related species that should be carefully compared with similar material reported from comparable habitats in Russia. It has been commonly collected from middle-elevation, calcareous, shrubland habitats dominated by *Artemisia* spp. and/or *Atriplex* spp. in Utah, Wyoming, Idaho, and Colorado. Weber (1967) suggested this species is an environmental modification of *Aspicilia calcarea*. Roger Rosentreter's work on the vagrant *Aspicilia/Agrestia* spp. of western North America will undoubtedly show that there are at least several new species records for North America from this group.

***Aspicilia reptans* (Looman) Wetm.** A fruticose, semi-vagrant species collected from middle-elevation calcareous sites in Idaho and Wyoming and alpine tundra sites in Utah. This species is commonly overlooked because it blends in with detritus that tends to accumulate in the above-mentioned habitats. This species represents one extreme of the Agrestia-Aspicilia complex, a group requiring serious monographic treatment.

***Aspicilia* sp.** A fruticose, vagrant species collected from short-grass–shrubland steppe sites in Wyoming and Idaho. This species most closely resembles *Agrestia hispida;* however, this taxon has a more substantial central thallus with short, blunt lobes rather than the densely and finely branched thalli typical of *Agrestia hispida*. In addition, *A. hispida* has better developed and more prominent pseudocyphellae. Thalli of *Aspicilia* sp. are also more compact and tend to be more spherical in shape. Roger Rosentreter's work comparing North American members of this group with similar Russian taxa will likely result in an epithet for this species.

***Buellia elegans* Poelt.** A squamulose species with prominent lobes. This species is broadly distributed, reaching its best development in sites protected from trampling. It has been collected from protected sandy soils in Emery County, Utah, as well as gypsiferous soils in Colorado, Utah, and northwestern Arizona, and less commonly from protected calcareous soils in the Great Basin.

***Caloplaca tominii* Saviez.** A crustose, sorediate species that occurs commonly on calcareous soils throughout the Great Basin. This species was first reported by Nimis (1981) as new to North America. His collections were from the Kluane region of the Canadian Yukon, an area in some respects strikingly similar to the open shrublands of the Great Basin.

***Catapyrenium daedaleum* (Krempelh.) B. Stein in Cohn.** A rather rare squamulose species collected from middle- to higher-elevation, calcareous sites in Colorado, Wyoming, and Utah.

***Catapyrenium lachneum* (Ach.) R. Sant.** This squamulose lichen is one of the most broadly distributed terricolous species in the Intermountain Area. It commonly occurs on calcareous soils in the Great Basin, middle-elevation pinyon-juniper sites, gypsiferous soils of the Colorado Plateau, and alpine tundra soils. This species has an incredible ecological amplitude and demonstrates substantial morphological variation.

***Collema tenax* (Swartz) Ach.** This isidiate, squamulose lichen is one of the most common terricolous lichens of the Intermountain Region. It occurs on calcareous soils in the Great Basin and also on gypsiferous soils on the Colorado Plateau. This species recovers very rapidly following perturbation (e.g., fire or grazing disturbance). Its capacity for quick recovery is likely related to the fact that it produces abundant vegetative propagules (isidia) (Johansen et al. 1984, Johansen and St. Clair 1986).

***Dermatocarpon miniatum* (L.) Mann.** This foliose, usually attached saxicolous lichen occasionally becomes detached and occurs as a vagrant on the soil. According to Rosentreter and McCune (1992) most vagrant *Dermatocarpon* species are collected from poorly drained basalt flats dominated by *Artemisia rigida* in western Idaho and eastern Washington and Oregon. After careful study Rosentreter and McCune have determined that vagrant species of *Dermatocarpon* are detached fragments of either *D. reticulatum* or *D. miniatum;* therefore, they recommend that the epithet for the vagrant form of this species (*Dermatocarpon vagans* Imsh.) no longer be used.

***Dermatocarpon reticulatum* Magn.** This foliose, usually attached saxicolous species is reported as a vagrant soil lichen from northwestern Wyoming, western Idaho, and eastern Oregon. See related dicussion under *Dermatocarpon miniatum*.

***Diploschistes diacapsis* (Ach.) Lumbsch.** A crustose lichen commonly collected on gypsiferous soils in southern Utah, southeastern Colorado, and northwestern Arizona. This species is the single most abundant lichen collected from gypsiferous soils in the Intermountain Area.

***Endocarpon pusillum* Hedwig.** This squamulose species is broadly distributed but not particularly common. It is found on calcareous soils in the Great Basin and occasionally on undisturbed, sandy soils in pinyon-juniper communities. The fact that this species is rather uncommon may, at least in some measure, be related to a relatively low tolerance for grazing and fire disturbance.

***Fulgensia desertorum* (Tomin) Poelt.** This granular-subsorediate lichen occurs commonly on gypsiferous soils in Arizona, Colorado, and Utah.

***Fulgensia fulgens* (Swartz) Elenkin.** A squamulose species with well-developed lobes. It is frequently collected from calcareous soils of the Colorado Plateau, gypsiferous soils, and less commonly from undisturbed calcareous soils in the Great Basin.

***Gypsoplaca macrophylla* (Zahlbr.) Timdal.** This rather rare squamulose lichen has recently been collected from gypsiferous soils in southwestern Colorado and was reported as new to North America by Timdal (1990). Likely, with additional collections and more careful analysis of existing collections, other species will be added to this genus. This taxon was also collected from gypsiferous soils on the San Rafael Swell in Emery County, Utah, during the fall of 1992 and represents a new species record for the state (BRY C21698).

***Psora cerebriformis* W. Weber.** A robust, squamulose lichen frequently collected from pinyon-juniper and shrubland habitat in Arizona, Colorado, Idaho, Nevada, New Mexico, Utah, and Wyoming.

***Psora crenata* (Taylor) Reinke.** A squamulose lichen with prominent, marginal apothecia. This species is rare to common on calcareous and gypsiferous soils in Arizona, Colorado, New Mexico, and Utah.

***Psora decipiens* (Hedwig) Hoffm.** This squamulose lichen, along with *Catapyrenium lachneum*, is the most broadly distributed terricolous lichen in western North America. It has been commonly collected from calcareous soils in the Great Basin, gypsiferous soils on the Colorado Plateau, and high-elevation alpine tundra sites throughout the Rocky Mountains. It occurs less commonly on soils in pinyon-juniper habitat.

***Psora globifera* (Ach.) Massal.** A squamulose lichen that generally occurs in fissures of calciferous rocks. It also occasionally occurs on calcareous soils in Arizona, Colorado, Idaho, Nevada, Utah, and Wyoming.

***Psora icterica* (Mont.) Müll. Arg.** A squamulose soil lichen commonly collected in the arid areas of the western United States. In the Intermountain Area it has been reported from Arizona, New Mexico, and Colorado. It often occurs in pinyon-juniper habitat on sandy, undisturbed soils.

***Psora luridella* (Tuck.) Fink.** A rare, squamulose lichen reported from Colorado, New Mexico, [illegible] Utah. Because *P. luridella* is morphologically similar to *P. globifera*, the two species [illegible]

***Psora montana* Timdal.** A squamulose soil lichen [illegible] below timberline. It is [illegible] Utah, and Wyoming.

***Psora* [illegible] A. Schneider.** This squamulose [illegible] the southwestern [illegible] Area it has been reported from Arizona and southwestern Colorado.

***Psora tuckermanii* R. Anderson *ex* Timdal.** This broadly distributed, squamulose soil lichen has been reported for Arizona, Colorado, Idaho, Nevada, New Mexico, Utah, and Wyoming. *P. tuckermanii* shows extensive morphological variation and is commonly confused with several other species of *Psora*. It has been commonly collected from calcareous soils in the Great Basin as well as on soil over rock on the Colorado Plateau.

***Rhizoplaca haydenii* (Tuck.) W. Weber.** A vagrant soil lichen collected from calcareous shrubland habitats in Idaho, Utah, and Wyoming. This species demonstrates substantial morphological variation ranging from robust spherical thalli (typical of lower-elevation sites) to finely branched flattened thalli (typical of higher-elevation sites). The genus *Rhizoplaca* needs attention and is presently under review by Bruce Ryan.

***Squamarina lentigera* (Weber) Poelt.** This squamulose soil lichen has prominent lobes. *S. lentigera* is one of the more abundant lichens collected from gypsiferous habitats in northern Arizona, southwestern Colorado, and southern Utah. It has also been collected from undisturbed, sandy soils in pinyon-juniper habitat.

***Toninia caeruleonigricans* (Lightf.) Th. Fr.** A convoluted, crustose to squamulose soil lichen commonly collected from calcareous soils in the Great Basin and Colorado Plateau. This species is one of the more broadly distributed soil lichens, occurring in Arizona, Colorado, Idaho, Nevada, New Mexico, Utah, and Wyoming.

***Toninia tristis* (Th. Fr.) Th. Fr.** A convoluted, squamulose soil lichen. This species occurs on calcareous soils and has been collected rarely from protected habitats in pinyon-juniper communites. It has been reported from Arizona, Colorado, New Mexico, and Utah.

***Xanthoparmelia chlorochroa* (Tuck.) Hale.** A foliose, vagrant lichen that occurs abundantly on soils of shrubland-steppe communities and less commonly in pinyon-juniper communities. The distribution of this species seems to be positively correlated with grazing impact (McCracken et al. 1983). It commonly occurs with *Agrestia hispida* and has been reported from Arizona, Colorado, New Mexico, Nevada, Utah, and Wyoming. Recently, this group has been split into several closely related species based on subtle morphological and chemical differences (Hale 1990). Only one of the chemical segregates is included here (*X. lipochlorochroa*). Further evaluation of vagrant *Xanthoparmelias* in the Intermountain Area will ultimately yield several additional species.

***Xanthoparmelia idahoensis* Hale.** A loosely attached to vagrant, foliose to sub-fruticose lichen collected from calcareous lacustrine ash soils near Salmon, Idaho. This rare but locally abundant lichen has been reported only from the type locality. Examination of similar habitats elsewhere should reveal a broader distribution pattern.

***Xanthoparmelia lipochlorochroa* Hale & Elix.** A rare, vagrant soil lichen that is a fatty acid chemotype of *X. chlorochroa*. The two species intermix in the desert shrublands of southwestern Wyoming. Careful examination of the chemistry of collections of *X. chlorochroa* will likely demonstrate a much broader distribution pattern for *X. lipochlorochroa*.

***Xanthoparmelia wyomingica* (Gyelnik) Hale.** A loosely attached, foliose lichen common on rocky soils in middle- to higher-elevation sites in Colorado, Idaho, Utah, and Wyoming. Hale (1990) indicates that this species does not occur below 3000 m and does not occur sympatrically with *X. chlorochroa*. However, I (St. Cl.) have personally collected this species from higher-latitude sites below 3000 m (northern Colorado, Idaho, and Wyoming); I have also observed that it often occurs sympatrically with *X. chlorochroa* in many of the higher-latitude sites.

Human-related Impact on Soil Crust Communities

Lichens are important components of soil crust communities in the intermountain western United States, especially in areas protected from domestic grazing, wildfire, and off-road vehicle activity. Soil crusts in general and the lichen component in particular tend to be very sensitive to human-related perturbation. These complex, sensitive communities thrived for years prior to the advent of modern humans. They provide 40–100% of the ground cover in an area with relatively sparse vascular plant cover. They also effectively reduce wind and water erosion while significantly increasing soil fertility. However, over the last 150 years a significant portion of the soil crust communities of the Great Basin and Colorado Plateau has been heavily damaged, mostly due to intensive grazing by cattle and sheep. Soil crust communities are generally slow to recover, often requiring many years for full recovery (Anderson, Harper and Rushforth 1982, Johansen et al. 1984).

Soil crust community structure in the Intermountain Area evolved without significant impact from large herds of grazing animals (i.e., bison) and with little or no impact from wildfire (Mack and Thompson 1982). Impact from herds of deer, antelope, and elk was minimized due to the smaller size and number of herds and the time of the year they inhabited semiarid regions of the Great Basin and Colorado Plateau. These herds always occupied lower-elevation sites during the winter and early spring months when soil crusts were wet because of seasonal precipitation and thus less vulnerable to the effects of trampling. However, as the drier summer months approached and soil crusts became dry and brittle, and thus more vulnerable to trampling, wild grazing animals moved back into the mountainous areas of the region. In contrast, modern humans have maintained larger herds of domestic animals in greater numbers and have grazed the basin and plateau regions well into the summer months or even continuously. Furthermore, modern humans have introduced alien vascular plant species that now make it possible to sustain large wildfires in a region where wildfire was not particularly common. The end result has been extensive damage to soil crust communities with a concomitant increase in soil erosion and decline in soil fertility.

Many species of lichens are sensitive to various types of air pollutants (Nash and Wirth 1988). Recently, they have been used to biomonitor the effects of air pollution in protected habitats such as wilderness areas and national parks (St. Clair 1989). Unfortunately, very little is known about the effects of air pollutants on soil crust lichens. It is generally thought that the basic soils of the Intermountain Area ameliorate the effects of air pollution, especially acid-generating pollutants. Even though no empirical evidence supports this hypothesis, researchers have shown that lichens growing on calcareous substrates do have a higher tolerance for acid pollution. Currently, a study is in progress to evaluate the effects of emissions from a toxic waste incinerator in central Utah on soil crust communities. Baseline community data and toxic element concentrations from the soil were obtained prior to operation of the incinerator. Follow-up studies will show whether or not toxic emissions accumulate in the soil and/or negatively impact soil crust communities. Research is also needed to accurately evaluate the effects of acid precipitation on soil crust communities in general and the lichen component in particular. Failure to document air pollution effects could further jeopardize a resource that has already sustained significant damage from intensive grazing and wildfire.

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BRYOPHYTES ON THE CALCAREOUS SOILS OF MUNGO NATIONAL PARK, AN ARID AREA OF SOUTHERN CENTRAL AUSTRALIA

A. J. Downing[1] and P. M. Selkirk[1]

ABSTRACT—Bryophytes were found to be abundant as components of microbiotic soil crusts on the calcareous soils of Mungo National Park, an arid area of southern central Australia. Six sites that reflected differences in soils, topography, and vascular plant vegetation were studied. At each site bryophytes were abundant, both in terms of number of species present and percent ground cover. Number of species present did not differ significantly between sites, but percent bryophyte cover was lower at a site on sand dunes in mallee woodland and a site on a silcrete ridge than at the four other sites. Environmental factors (soil texture, pH, conductivity, nutrient status, vascular plant vegetation, light level, leaf litter, and fire frequency) appear to play a significant part in determining bryophyte distribution. Mosses that occur at Mungo are also widespread on calcareous substrates throughout arid southern Australia.

Many of the bryophyte species present at Mungo also occur on limestones in high rainfall areas of eastern Australia. Environmental factors favoring bryophytic soil crusts in arid Australia are also present on limestones in high rainfall areas of eastern Australia and may account for the presence of many arid zone bryophyte species on limestones. In Australia there appears to be a relationship between rainfall and the ratios of acrocarpous to pleurocarpous mosses, and thallose to leafy liverworts. Recognition of calcareous soils, widespread in arid areas of southern Australia, may be possible by assessing a combination of characteristics of bryophyte assemblages.

Key words: arid lands, Australia, bryophytes, calcareous soils, limestones, microbiotic crusts

This investigation of bryophyte distribution at Mungo National Park was undertaken as part of a wider study to determine whether there is a suite of bryophytes consistently associated with calcareous soils in Australia, and whether it is possible to determine the calcareous nature of a substrate by the associated bryophytes. Many bryophyte species that occur on limestones in the high rainfall areas of eastern Australia are more usually associated with arid areas of Australia (Downing 1992, Downing et al. 1991). This study considers the relationships between bryophytes of arid areas of southern Australia and bryophytes on limestones in the relatively high rainfall areas of eastern Australia.

Mungo National Park (33°45′S, 142°59′E, 91 m.a.s.l.) lies within the Australian arid zone (Fig. 1) and is well known for its significance in Aboriginal prehistory, with Aboriginal occupation dating back to 40,000 y.b.p. Prior to 1922 the present Mungo National Park was part of a property of 203,000 ha carrying approximately 50,000 sheep. The property was subsequently divided into smaller holdings; and, in 1978, the holding known as Mungo was purchased by the New South Wales National Parks and Wildlife Service. In 1979 Mungo was officially declared a national park and was extended in 1984 when Zanci, the adjoining property to the north, was added to the park. Sheep and cattle were removed from Mungo in 1978; their absence was important in our selection of a study area, as observations of bryophytes on limestones and siltstones at Attunga in eastern Australia indicate that the presence of sheep changes the nature of bryophyte assemblages (Downing 1992). Graetz and Tongway (1986) have shown that removal of microbiotic soil crusts by heavy grazing causes changes in soil structure and chemistry which are significant for plant growth. Overseas studies (Brotherson et al. 1983, Johansen and St. Clair 1986, Kleiner and Harper 1972) have shown that severe trampling by grazing animals can be the most damaging hazard of microbiotic crusts in North American deserts.

Lake Mungo lies on the flat plains of the Murray Basin, a shallow sedimentary basin created by subsidence at the beginning of the

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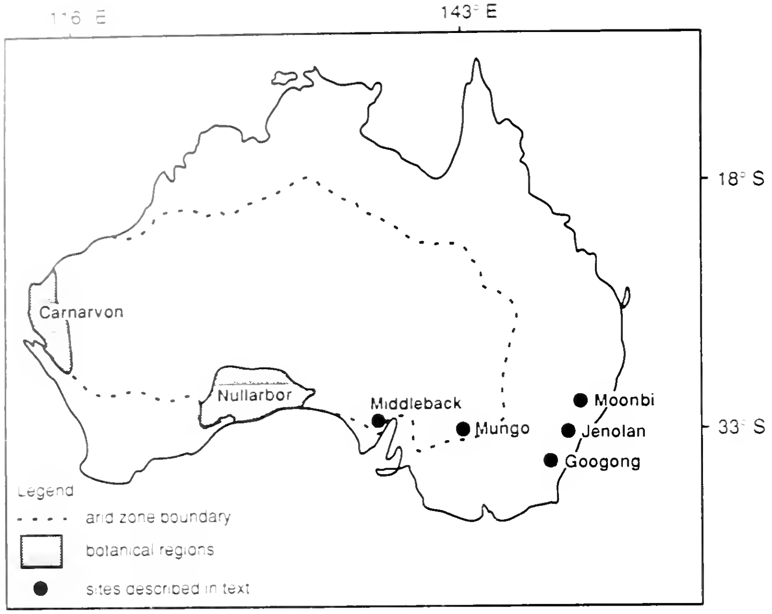

Fig. 1. Map of Australia showing location of Carnarvon and Nullarbor Botanical regions and sites described in the text in relation to the Australian Arid Zone.

Tertiary, now consisting of Quaternary aeolian sediments overlying Tertiary marine sequences (Geological Survey of NSW 1971). Fluvial and lacustrine sediments were deposited during the Pleistocene, and these are overlain by Quaternary sandy to clayey calcareous sediments, the most widespread surface geological formation of the Murray Basin (Northcote 1980).

Calcareous materials are a significant feature of the area, and calcium carbonate ($CaCO_3$) can be present (3–30%) in soils as "fine earth carbonate." Calcium carbonate can be present also as [illegible] nodules, which are soft to very hard [illegible] of calcium carbonate cemented [illegible] (75–85% calcium carbonate) in a usually [illegible] soil mix (Goudie 1983). The [illegible] horizons of most soils in the area are [illegible] calcareous earths have pH [illegible] and 8.5. Deep sands are [illegible] pH values close to [illegible] can be as low [illegible] other soils, with the maximum [illegible] horizons where there is the [illegible] accumulation of calcium carbonate [illegible] (0.06%) in the A horizons [illegible] low [illegible] (Walter [illegible] low [illegible] 1980).

Phosphorus content is always low (<0.001%) and is correlated with soil texture (Northcote 1980, Stafford Smith and Morton 1990).

Lake Mungo, a vast, dry lake, is the principal landform of Mungo National Park. The lunette or crescent-shaped ridge that flanks the eastern shore of Lake Mungo and dominates the landscape is visible from the air as far as 100 km away. The base of the lunette is composed of clay, silt, and sand, topped by mobile siliceous sands.

The lake floor consists of yellow-grey cracking clays. To the west of the lake and to the southeast of the lunette are open plains of brown calcareous earths. On the northeastern side of the lunette are subparabolic dunes of siliceous sands (Eldridge 1985). A low silcrete ridge runs through the northwestern section of the lake. This is the only site within the park where rock (excluding calcrete rubble) is found, and the hard silcrete rock has been a valuable resource for stone tool manufacture by Aboriginal people.

Mungo lies within the arid zone of Australia as defined by Meigs (1953), with the southern boundary of the Australian Arid Zone following the 250-mm rainfall isohyet, the eastern and northern boundary following the 375-mm isohyet, and the Indian Ocean forming the boundary in the west (Fig. 1).

TABLE 1. Climatic data. Mean monthly maximum and minimum temperatures (°C) for Mildura, 34°14'S, 142°05'E, 95 km SW of Mungo National Park: m.max = mean maximum temperature, m.min = mean minimum temperature (Bureau of Meteorology 1975). Average monthly rainfall in mm for Pooncarie, 33°22'S, 142°35', 56 km NW of Mungo (Bureau of Meteorology 1975). Rdays = number of rain days.

	J	F	M	A	M	J	J	A	S	O	N	D	Yearly
Temperature													
m.max (°C)	32	31	28	24	19	16	15	17	20	24	27	30	24
m.min. (°C)	17	16	14	11	7	5	4	5	7	10	12	15	10
Rainfall													
Mean (mm)	21	20	17	18	26	27	21	24	21	26	20	21	262
Median (mm)	9	8	9	10	18	19	18	20	15	18	10	11	246
Rdays	3	2	2	3	4	5	5	5	4	4	3	3	43

Mungo National Park has hot, dry summers and cool winters (Table 1—records for Mildura, closest temperature-recording station). Taking into account its more northerly location, mean monthly temperatures at Mungo are likely to be 1–2°C higher than those of Mildura. Frosts are common during the cooler months of the year.

Rainall averages for Pooncarie, 33°22'S, 142°35'E (closest rainfall recording station to Mungo; Table 1), recorded over 103 years indicate an evenly distributed rainfall (Bureau of Meteorology 1989a). However, in arid Australia, where there is considerable variation in rainfall from year to year, the mean is often much higher than the median, and thus the median rainfall value is a more reliable indicator of a typical year (Bureau of Meteorology 1989a). Mungo falls within an area of moderate to high rainfall variability (Bureau of Meteorology 1989b).

Mungo National Park lies within the Eastern Mulga Region of Arid Australia (Jessop 1981). The vegetation of Mungo National Park has been well documented by Rice (1986), who recognized four vegetation types: lakebed chenopod shrubland, *Heterodendrum/Casuarina* woodlands, mallee woodlands, and lunette vegetation.

METHODS

Six sites that reflected differences in topography, soils, and vascular plant vegetation were selected for study (Fig. 2). At each site a 10-m-long transect was set out. Along this transect, two adjacent rows of 1-m² quadrats were studied, giving a total of twenty 1-m² quadrats for each site. Direction and slope of each transect were recorded. Fieldwork was carried out in May and October 1991.

Site A: 33°43'45"S, 143°01'15"E, 98 m.a.s.l. western shore of Lake Mungo. An eroded area close to Mungo homestead and shearing shed. Calcareous brown earth soils. Chenopod shrubland with *Maireana pyramidata* (Benth.) P. G. Wilson (black blue bush) and occasional *Casuarina cristata* Miq. ssp. *pauper* (F. Muell. ex Miq.) L. A. S. Johnson (belah).

Site B: 33°44'44"S, 143°07'24"E, 68 m.a.s.l. lake floor, SW of Walls of China. Yellow-grey cracking clays. Chenopod shrubland with *Maireana pyramidata* and sparse grasses.

Site C: 33°45'10"S, 143°07'30"E, 70 m.a.s.l. lunette, eastern lake shore, N of Grand Canyon track. Yellow-grey cracking clay but with more sand on the surface than at site B. Chenopod shrubland with *Maireana pyramidata* and grasses.

Site D: 33°47'14"S, 143°07'40"E, 82 m.a.s.l. belah woodland. On the plain to the east of the lunette. Uneroded calcareous brown earth. *Heterodendrum oleifolium* Desf. *Casuarina cristata* woodland with *Maireana pyramidata* and *Enchylaena tomentosa* R. Br. as undershrubs.

Site E: 33°43'55"S, 143°10'20"E, 88 m.a.s.l. mallee/dune. Dune crest in subparabolic dunes. Red siliceous sand. Mallee woodland of *Eucalyptus socialis* F. Muell. ex Miq., *E. foecunda* Schauer, *E. dumosa* A. Cunn. ex Schauer ssp. *dumosa*, and *Triodia irritans* R. Br. var. *laxispicata* N. T. Burb. (spinifex grass).

Site F: 33°43'16"S, 143°02'26"E, 73 m.a.s.l. silcrete ridge, NW lake floor. Yellow-grey cracking clays. Outcropping silcrete rock embedded in the soil and scatterings of stone chips and flakes on the surface of the soil. Chenopod shrubland, including *Maireana pyramidata*, *M. sedifolia* (F. Muell.) P. G. Wilson (pearl blue

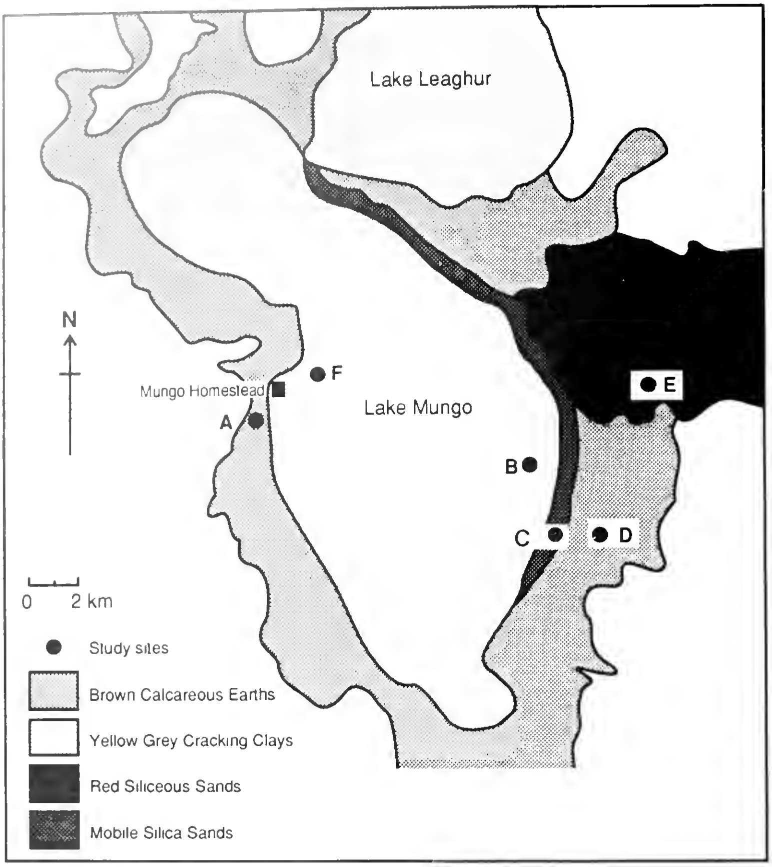

Fig. 2. Map of Lake Mungo and surroundings showing location of six study sites. A–western lake shore, B–lake floor, C–lunette, D–belah woodland, E–mallee/dune, F–silcrete ridge.

bush), and *Atriplex vesicaria* Heward ex Benth. (bladder saltbush).

Because of their small size (<5 mm), bryophytes present at Mungo could only be identified to species level after microscopic examination in the laboratory. The presence of a species within a quadrat was recorded and is referred to as an "occurrence." In addition to bryophyte species recorded from transect sites, a species list was compiled for the park. Bryophytes were collected also from a gypsum (calcium sulphate) "copi" mound, approximately 16 km [illegible] Pooncarie (33°24'S, 142°41'E).

Percentage bryophyte cover was estimated for each quadrat. Estimates were also made of percentage cover of bare soil, vascular plants, leaf litter, [illegible] calcium carbonate nodules [illegible] rock on silcrete ridge. Soil [illegible] the first, fifth, and tenth [illegible] samples were tested for reaction to 0.5 M HCl, for electrical conductivity, and for pH(H_2O).

Because many bryophytes of arid regions are ephemerals, additional soil was collected from each site. Pots of soil were maintained in an unshaded glasshouse at Macquarie University, watered with distilled water, and kept covered with sheets of glass to minimize invasion by glasshouse bryophyte species. Specimens growing from propagules present in the soil were recorded.

Bryophyte specimens were identified using published keys and descriptions, particularly those in Catcheside (1980), Scott (1985), Scott and Stone (1976), Beever (1988), and Sainsbury (1971). Assistance from specialists was obtained in identifying some difficult specimens. The names of bryophytes in this study for the most part follow Streimann and Curnow (1989) and Scott (1985). *Didymodon subtorquatus* (C.

TABLE 2. Number of occurrences of each species and bryophyte percent (± standard deviation) recorded from the transect at each site at Mungo National Park. A western lake shore, B lake floor cover, C lunette, D belah woodland, E–mallee/dune, F–silcrete ridge. Each transect consists of twenty 1-m^2 quadrats. Maximum number of occurrences possible per site = 20. ° indicates species cultivated.

Species collected	A	B	C	D	E	F	Total
1. *Didymodon torquatus*	°20	20	20	20	18	°20	118
2. *Bryum pachytheca*	°20	19	13	°20	°4	°17	93
3. *Desmatodon convolutus*	8	18	11	19	18	12	86
4. *Crossidium geheebii*	7	20	19	20	1	4	71
5. *Crossidium davidai*	10	12	7	17	1	11	58
6. *Aloina bifrons*	5	3		19	3	13	43
7. *Gigaspermum repens*	—	1		19	12		32
8. *Barbula hornschuchiana*	°	4		°20		3	27
9. *Pterygoneurum ovatum*	1	4		8	1		14
10. *Bryum argenteum*	2	—	7	—			9
11. *Riccia lamellosa*	°1	°18	°	°20			39
12. *Riccia limbata*	°	°4	°	°2	°		6
Total number of occurrences at each site	74	123	77	184	58	80	596
Additional cultivated species							
13. *Funaria glabra*	°						
14. *Riccia cavernosa*		°	°	°			
15. *Riccia crystallina*		°	°	°			
Total number of species recorded for each site transect	12	13	10	13	10	10	
Bryophyte % cover ± sd	39 ± 19	28 ± 13	31 ± 12	38 ± 18	2 ± 2	9 ± 3	

Muell. & Hpe) Catches. and *Didymodon luehmannii* (Broth. & Geh.) Catches. are included in *Didymodon torquatus*. Where these species occurred together, it proved impossible to separate them into three distinct taxa. One of the most commonly occurring species of *Tortula* in Australia is usually referred to as *T. princeps* de Not., which Kramer (1988) concludes does not occur in Australia. This study follows Kramer (1988) in his use of *T. antarctica*. Distinguishing specimens of *Desmatodon convolutus* from *Crossidium davidai* proved to be extremely difficult. The number of cells of the filaments of the adaxial surface of the costa was selected as the distinguishing feature: plants with filaments consisting of one cell were assigned to *Desmatodon convolutus*, those with filaments of more than one cell to *Crossidium davidai*.

RESULTS

Bryophytes were found to be abundant components of the microbiotic soil crusts on most soils within Mungo National Park, accounting for up to 80% cover within some quadrats. The crust in most places was reddish brown and short (<2 mm high). Crustose lichens (e.g., *Psora decipiens* Hoffm.) were often a conspicuous component of the crusts. However, microbiotic crust was not present on the mobile silica dunes of the lunette nor where grasses were well established. Tongway (unpublished) has described a succession from microbiotic soil crust to grassland, which eventually leads to elimination of the microbiotic soil crust as grasses dominate the landscape.

Four sites, western lake shore (A), lake floor (B), lunette (C), and belah (D), had similar cover, with means ranging from 28% to 39% (Table 2). Two sites, mallee/dune (E, 2%) and silcrete ridge (F, 9%) had significantly less cover than the other sites and were different from each other.

A total of 15 bryophyte species were recorded from the transect sites. Ten moss species and two liverworts were collected from the transect sites. One additional moss and two additional liverworts were cultivated in the glasshouse pot trials.

There was little difference in the number of species that occurred at each site (Table 2). Two sites, the lake floor (B) and belah (D), were different from each other but had significantly more occurrences per quadrat than the western lake shore (A), lunette (C), mallee/dune (E), and silcrete (F).

The moss flora consisted exclusively of acrocarpous mosses. Pottiaceae was the dominant family, not only in number of species present (7 [illegible] at Mungo National [illegible] Pooncarie [illegible] occurred [illegible]

[illegible]	[illegible]
[illegible]	*Aloina aloides* (Schultz) Kindb. var. *ambigua* (B.S.G.) Craig *Aloina bifrons* (De Not.) Delgadillo *Barbula crinita* Schultz *Barbula hornschuchiana* Schultz *Crossidium davidai* Catches. *Crossidium geheebii* (Broth.) Broth. *Desmatodon convolutus* (Brid.) Grout *Desmatodon recurvatus* (Hook.) Mitt. *Didymodon torquatus* (Tayl.) Catches. *Pterygoneurum ovatum* (Hedw.) Dix. *Tortula antarctica* (Hpe.) Wils. *Tortula pagorum* (Milde) de Not. *Tortula papillosa* Wils. *Trichostomopsis australasiae* (Hook. & Grev.) H. Rob.
BRYACEAE	*Bryum argenteum* Hedw. *Bryum campylothecium* Tayl. *Bryum dichotomum* Hedw. **Bryum pachytheca* C. Muell.
FUNARIACEAE	*Funaria glabra* Tayl. *Funaria hygrometrica* Hedw.
FISSIDENTACEAE	*Fissidens vittatus* Hook. f. & Wils.
GIGASPERMACEAE	*Gigaspermum repens* (Hook.) Lindb.
RICCIACEAE	*Riccia albida* Sull. ex Austin *Riccia asprella* Carring. & Pears. *Riccia cavernosa* Hoffm. *Riccia crinita* Taylor *Riccia crystallina* L. *Riccia lamellosa* Raddi *Riccia limbata* Bisch. *Riccia nigrella* DC. *Riccia rorida* Na Thalang *Riccia sorocarpa* Bisch.

[illegible] of 5 total bryophyte species, but also in number of occurrences (419 of 596, 70%). Two species [illegible] accounted for 102 occurrences [illegible]

[illegible] consisted exclusively of [illegible] the Ricciaceae. Two [illegible] and *R. lamellosa*, were [illegible] each transect site. [illegible] two ephemeral [illegible] soil from the lake floor [illegible] D).

There [illegible] sites in terms of [illegible] each transect site [illegible] occurred at each transect site [illegible] species

TABLE 4. pH and EC (electrical conductivity) in 1:5 soil to water extracts (μS/cm = microsiemens/centimeter) of each transect site, and Pooncarie gypsum. + indicates soil effervesced with HCl.

Transect site	pH	EC (1:5) (μS/cm)	Reaction to 0.5 M HCl
A. Western lake shore	9.0	0.12	+
B. Lake floor	9.0	0.12	+
C. Lunette	9.0	0.05	+
D. Belah	9.0	0.06	+
E. Mallee	6.5	0.02	−
F. Silcrete	8.5	0.04	−
Pooncarie gypsum	9.0	1.51	+

accounted for 71% of total number of occurrences (426/596). *Didymodon torquatus* occurred most frequently, being present in 118 of a possible 120 quadrats. *Bryum pachytheca* occurred in 93 quadrats. *Gigaspermum repens* was recorded at three of the six sites and also on the Pooncarie gypsum.

The 32 bryophyte species collected in Mungo National Park included 22 mosses and 10 liverworts (Table 3). The moss flora consisted exclusively of acrocarpous mosses. Pottiaceae was the dominant family and was represented by 14 species. The Bryaceae consisted of 4 species, Funariaceae 2 species, and *Fissidens vittatus* and *Gigaspermum repens* were present. It is probable that other ephemeral species grow from time to time within the park. The liverwort flora consisted of 10 species of *Riccia*.

DISCUSSION

Bryophytes were abundant in most of Mungo National Park as a component of microbiotic soil crusts. Two transect sites, the lake floor and belah, had significantly greater percent cover than the other four sites. Both are situated in flat, low-lying areas with fine-textured, stable soils that retain moisture for longer periods than the more elevated, and thus more freely draining, sites on the western lake shore—lunette, mallee, and silcrete ridge. Microbiotic crusts in arid regions have consistently been shown to be more abundant (percent cover) when soil texture is finer (West 1990). Soil pH (H_2O) for all sites with the exception of the mallee/dune varied from 8.5 to 9.0, and electrical conductivity was highest for the lake floor and western lake shore, closely followed by the belah and lunette sites (Table 4). Sodium chloride is known to enhance the growth of cyanobacteria, possibly being essential for some species; thus, higher salt concentrations in the floor of the lake may in fact enhance the development of microbiotic crust (West 1990).

Two sites, the mallee/dune and silcrete ridge, had significantly less bryophyte cover than the other sites. The silcrete ridge has less soil surface area for colonization by bryophytes because of outcropping silcrete rock and scattered stone flakes. Anderson et al. (1982) found less well-developed crust on rocky and sandy sites than on sites with fine-textured soils. Despite the fact that the soils of the silcrete ridge are yellow-grey cracking clays, similar to those of the lake floor, the ridge is also 2–3 m higher than the lake floor in which it occurs, allowing free drainage and lessening the retention of water in the soil. Bryophytes were not found on, or in crevices in, the silcrete rock, but lichens were conspicuous and abundant. *Grimmia* species are often present on rock in arid or semiarid environments in South Australia and Western Australia, and the presence of this genus was anticipated in this location. The small size of the rocky outcrop and its intensive use as a stone tool quarry by Aboriginal people may have played a part in the absence of this genus from the park.

The mallee site on the dune crest had lowest bryophyte cover (2%) of all sites studied. At this site the soil consisted of coarse, sandy soil, which was highly mobile and very freely draining. Soil pH(H_2O) and electrical conductivity were significantly lower than at the other sites (Table 4). Soil pH(H_2O) of the dune sand was 6.5, significantly lower than all other sites. This parallels the work of Anderson et al. (1982), who have shown that pH and soil texture are the apparent influential variables controlling the number of lichen and moss species in microbiotic soil crusts in Utah deserts. In their studies of a semidesert region in southern Utah, they found that both species diversity and abundance increase with an increase in fine soil particles (silt and clay). On dune crests in arid Australia sand is deeper and more mobile than it is on the swales between the dunes; it also retains less moisture. The nutrient status of dune crests—calcium, nitrogen, and organic matter—is significantly lower than that of dune swales (Buckley 1981, 1982). Stafford Smith and Morton (1990) reported significantly lower levels of nitrogen and phosphorus in sand dunes than in either calcareous earths with chenopod shrublands or cracking clays. The dune soil did not effervesce with acid, indicating much lower levels of calcium carbonate in the soil than at any other site (Table 4).

The *Eucalyptus* mallee woodland of the dune crests also appears to inhibit the survival of bryophytes, with lower light levels and more leaf litter than either chenopod shrublands or *Heterodendrum oleifolium* woodlands. Mallee woodlands have a higher fire frequency than either chenopod shrublands or *Heterodendrum*/*Casuarina* woodlands (Gill 1989, Hodgkinson and Griffin 1982, Noble 1989). High fire frequency also reduces cryptogam cover (Greene et al. 1990). *Gigaspermum repens*, however, grows well on the loose sand of the dune crests. It may be easier for underground stems to penetrate loose, coarsely textured sand than heavier, finer-textured soils and clays. In some quadrats *G. repens* appeared to form an underground network of stems, which must play an important part in maintaining soil stability. Underground stems may also enable *G. repens* to survive fire. Two epiphytic mosses, *Tortula pagorum* and *T. papillosa*, were collected from the bark of *Heterodendrum* and *Casuarina cristata*. Both trees have thick, corrugated bark, and the accumulated dust in crevices in the bark reacted with 0.05 M HCl and had a pH of 8.5. In all cases the mosses were on either the southern side of the tree or the undersurface of a branch. In dry conditions the mosses were barely visible, but bright green leaves opened within seconds of their being doused with water. *Tortula pagorum* was also collected from rough bark on the southern side of tree trunks and the undersurface of branches of *Eucalyptus largiflorens* F. Muell. (black box) growing in box swamps on the Mungo to Pooncarie road.

Tortula antarctica, *Barbula crinita*, and *Bryum campylothecium* were present at Mungo only in protected habitats. All three occurred occasionally under the protective "skirt" on the southern side of a *Triodia irritans* var. *laxispicata* tussock and in sheltered, low-lying areas such as a terraced section of lake floor to the NW of the Mungo homestead. Two liverworts, *Riccia nigrella* and *R. sorocarpa*, were collected from this location only.

Two locations had a bryophyte assemblage that included a number of introduced and cosmopolitan species. Bryophytes collected in the vicinity of the original Mungo homestead and lagoon shell included *Bryum argenteum*, *B. dichotomum* (wet area at base of a concrete tank stand), and *Trichostomopsis australasiae*. Bryophytes collected from damp sand in the vicinity of Vigars Wells (once a staging post for Cobb & Co. coaches on the NE side of the lunette) included *Bryum argenteum*, *Funaria hygrometrica*, and *Trichostomopsis australasiae*.

Six mosses and one liverwort were collected from the gypsum site at Pooncarie and two additional liverworts were cultivated (Table 3). The species list is very similar to that of Mungo National Park. Two species collected at Pooncarie, *Riccia albida* and *Aloina aloides* var. *ambigua*, were not present on the calcareous soils of Mungo National Park. Scott (1985) records the habitat for *Riccia albida* as being predominantly on gypsum-rich soils. *Aloina aloides* var. *ambigua* may be an introduced species (Catcheside 1980), and its presence may be a result of the nearby busy road and stock route.

In summary, bryophytes of Mungo National Park appear to be most abundant where soils are low lying, stable, fine textured, with high pH, high electrical conductivity, and high levels of calcium, nitrogen, phosphorus, and organic matter and where vascular plants contribute least shading (i.e., light levels are high), least leaf litter, and lowest fire frequency.

It is interesting to compare the species list of mosses collected in Mungo National Park with species lists of mosses recorded from other areas within the Australian Arid Zone. A recent study (Stoneburner et al. in press) has provided a valuable census of mosses for the Botanical Regions of Western Australia. The boundaries of two of these regions, Carnarvon and Nullarbor, approximate the boundaries of the Carnarvon and Eucla sedimentary basins respectively (Fig. 1). The calcareous soils and underlying limestone rocks that dominate these basins were deposited as marine sediments during the Tertiary. Annual rainfall is approximately 200–300 mm in the Carnarvon Botanical Region and 150–200 mm in the Nullarbor Botanical Region.

A [illegible] list has also been compiled [illegible] Field Centre (32°57′S, 137°2[illegible]′E [illegible] Australia; Bell 1980, Howarth [illegible]). Research station soils are [illegible] calcareous [illegible] and concretions of [illegible] are [illegible] of the [illegible] limit of the Australian Arid Zone, has an annual rainfall of 200 mm, and lies within the Eastern Mulga Botanical Region (Jessop 1981).

There is a remarkable similarity between the assemblage of mosses at Mungo National Park and those within the Carnarvon and Nullarbor Botanical regions and at Middleback Field Centre (Table 5).

Many of the bryophytes collected from the calcareous soils of Mungo National Park are also present on limestones in high rainfall areas of eastern Australia. As at Mungo, the moss floras of three limestone sites in eastern Australia, Jenolan, Googong and Moombi, are dominated by acrocarpous species of Pottiaceae and Bryaceae. *Didymodon torquatus*, *Gigaspermum*

TABLE 5. Mosses of Mungo National Park and their occurrence within the Carnarvon and Nullarbor Botanical regions (Stoneburner et al. 1993) and Middleback Field Centre (Bell 1980, Howarth 1983), Australian Arid Zone. ○ present at this location.

Mungo	Carnarvon	Nullarbor	Middleback
POTTIACEAE			
Aloina aloides var. *ambigua*			
Aloina bifrons		○	○
Barbula crinita		○	○
Barbula hornschuchiana		○	○
Crossidium davidai	○	○	○
Crossidium geheebii	○	○	○
Desmatodon convolutus	○	○	○
Desmatodon recurvatus	○	○	○
Didymodon torquatus	○	○	○
Pterygoneurum ovatum	○	○	○
Tortula antarctica		○	○
Tortula pagorum		○	○
Tortula papillosa			
Trichostomopsis australasiae		○	○
BRYACEAE			
Bryum argenteum			○
Bryum campylothecium		○	○
Bryum dichotomum	○	○	○
Bryum pachytheca	○	○	○
FUNARIACEAE			
Funaria glabra			○
Funaria hygrometrica		○	○
FISSIDENTACEAE			
Fissidens vittatus	○	○	○
GIGASPERMACEAE			
Gigaspermum repens	○	○	○

repens, and *Fissidens vittatus* are present at each limestone site. The liverwort floras of these sites consist mostly of thallose liverworts from the order Marchantiales (Downing 1992, Downing unpublished data).

A comparison of bryophytes of Mungo National Park with those of limestone sites in high rainfall areas of eastern Australia indicates many species present at Mungo are also present on eastern limestones. Jenolan (33°47′S, 150°05′E) is located 792 m.a.s.l. and has an annual rainfall of 943 mm. Googong (35°31′S, 145°16′E) is 670 m.a.s.l. with a rainfall of 640 mm per annum, and Moonbi (30°56′S, 150°56′E) is 540 m.a.s.l. with rainfall of approximately 700 mm per annum. Of the bryophyte species collected at Mungo, 52% were collected also from Googong, 63% from Moonbi and Jenolan. Comparisons for mosses alone are more striking: 62% of Mungo species were also present at Googong, 71% at Moonbi, and 76% at Jenolan Caves (Table 6). Bryophytes were also more abundant on limestone substrates, both in percent ground cover and in number of species present, than they were on nearby non-calcareous substrates (Downing 1992).

At Mungo, microbiotic crusts are best developed where the soils are fine textured and have a high pH, high electrical conductivity, high levels of calcium, phosphorus, and nitrogen, high light levels, minimal leaf litter, and low fire frequency. Limestone soils are fine textured and high in calcium; they also have a high pH and high electrical conductivity. Where caves are present in limestone, phosphorus is often deposited as bat guano (Carne and Jones 1919, Lishmund et al. 1986). Where karst is well developed, limestones provide arid microenvironments even in high rainfall areas with precipitation in excess of 2000 mm per annum (Jennings 1985). The aridity of karst geomorphology is reflected in the lack of vascular plants, particularly trees (*Eucalyptus* spp.). In their absence, light levels are high, there is minimal leaf litter (Downing 1992), and fire frequency is reduced (Holland 1993). Thus, the environmental factors that promote the abundance of bryophytes on calcareous soils in arid environments are also present on limestones in high rainfall areas of eastern Australia.

At Mungo and at each eastern limestone location, the moss flora is dominated by acrocarpous mosses, and the liverwort flora is dominated by thallose liverworts of the order Marchantiales. Pleurocarpous mosses and leafy liverworts are present on limestones only where rainfall is greater than 650 mm per annum. Two families, Pottiaceae and Bryaceae, dominate the moss flora at each site, with *Gigaspermum repens* and *Fissidens vittatus* also present (Downing et al. 1991, Downing 1992, Downing unpublished data; Table 7).

Recognition of calcareous soils in southern Australia may be possible by assessing the abundance of bryophytes. The number of species and the percent cover on calcareous soils will exceed the number of species and cover on non-calcareous soils. Acrocarpous mosses (Pottiaceae, Bryaceae) and thallose liverworts (Marchantiales) will dominate the bryoflora, and a number

TABLE 6. Mosses of Mungo National Park and their occurrence on eastern Australian limestones (Downing et al. 1991, Downing 1992, Downing unpublished data). ° present at this location.

Mungo	Googong	Moonbi	Jenolan
POTTIACEAE			
Aloina aloides var. *ambigua*	°		
Aloina bifrons		°	°
Barbula crinita	°	°	°
Barbula hornschuchiana	°	°	
Crossidium davidai			
Crossidium geheebii	°	°	
Desmatodon convolutus			°
Desmatodon recurvatus	°		°
Didymodon torquatus	°	°	°
Pterygoneurum ovatum			
Tortula antarctica	°	°	°
Tortula pagorum	°	°	°
Tortula papillosa	°		°
Trichostomopsis australasiae			
BRYACEAE			
Bryum argenteum		°	°
Bryum campylothecium		°	°
Bryum dichotomum			°
Bryum pachytheca	°	°	°
FUNARIACEAE			
Funaria glabra		°	°
Funaria hygrometrica			
FISSIDENTACEAE			
Fissidens vittatus	°	°	°
GIGASPERMACEAE			
Gigaspermum repens	°	°	°

[illegible] of soil bryophyte assemblages on calcareous substrates (Downing et al. 1991, Downing [illegible]

	Jenolan (943 mm per annum)	Moonbi (700 mm per annum)	Mungo (246 mm per annum)
M[illegible]			
Acrocarp[illegible]	78%	100%	100%
P[illegible]ps	22%	0%	0%
P[illegible]	31%	38%	44%
B[illegible]	14%	29%	13%
[illegible]	Present	Present	Present
[illegible]	Present	Present	Present
[illegible]			
[illegible]	Present	Absent	Absent
[illegible] Marchantiales	Present	100%	100%

of key species will be present: *Didymodon torquatus*, *Bryum pachytheca* or *B. dichotomum*, *Gigaspermum repens*, and *Fissidens vittatus*.

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MICROBIAL SPATIAL HETEROGENEITY IN MICROBIOTIC CRUSTS IN COLORADO NATIONAL MONUMENT. I. ALGAE

Amy E. Grondin[1] and Jeffrey R. Johansen[2]

[illegible] Colorado National Monument [illegible] 24 [illegible] distances between samples were 0.013 to 10.0 [illegible] plots. Algal density varied [illegible] each distance class [illegible] less than [illegible] a scale of [illegible] the individual area of [illegible] rather [illegible] scale heterogeneity [illegible] wished to quantify [illegible]

Key words: [illegible] Colorado National Monument.

In the last half century numerous ecologists have studied natural distribution patterns of plants. Spatial distributions of populations are regular, random, or aggregated, with most species having aggregated distributions (Ludwig and Reynolds 1988). An issue of key concern to those interested in distribution is the size (length, area, or volume) of the sample taken to study distribution. Normally one wishes to use the smallest sample size possible that will still be representative of the population as a whole. In [illegible] samples are usually [illegible] representative sample size [illegible] (Goodall 1952 [illegible]) [illegible]

microbial ecologists have long been aware of heterogeneity in bacterial populations in the soil and generally take composite samples to avoid this problem (James and Sutherland 1939). In a recent study of soil algae of crusted soils of the Lower Columbia Basin (Johansen et al. 1993) we observed considerable heterogeneity in algal communities in undisturbed sites. In particular, we found that samples taken within 5 cm of each other appeared to be as different as samples taken several meters away. There was no correlation over time between algal densities at proximal sites, even though vascular plant cover demonstrated very clear patches on a scale much larger than 5 cm.

This study is an outgrowth of the work conducted in shrub-steppe in Washington. We had two goals at the outset of the project: (1) to document the scale of algal heterogeneity in soils that macroscopically appeared to be homogeneous, and (2) to report on the floristics of the soil algal community in a pinyon-juniper community in Colorado National Monument. We were not seeking to discover the variability in algae in crusted vs. noncrusted soils, or differences in algal density under various types of vascular plant cover; rather we wished to estimate

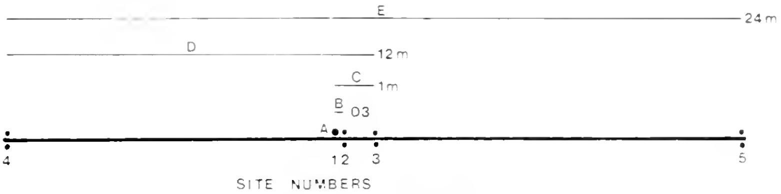


Fig. 1. Study site in canopy of Utah juniper in Colorado National Monument, Colorado. Site numbers (1–5) are given under the transect; groups of samples (A–E) and distances are given above the transect. Site 1 contained 16 samples; sites 2–4 contained 8 samples (two clusters of 4 at each point); site 5 contained 6 samples (two clusters of [illegible]

the algal heterogeneity within what one would consider in the field to be identical sites. A companion study on the spatial heterogeneity of bacteria and actinomycetes from the same site is reported by Wheeler et al. (1993). Recommendations regarding soil crust sampling methodology follow from this study.

MATERIALS AND METHODS

The study site is located in a pinyon-juniper community in Colorado National Monument, Colorado, USA. Sampling was conducted in early January 1989. Five plots on a transect 24 m long were chosen such that (1) they all contained pediceled, nonlichenized, soil algal crusts of similar appearance; (2) they all were under partial canopy of *Juniperus osteosperma* (Torr.) Little (Utah juniper); and (3) they were positioned such that plots or groups of plots were increasingly further apart, with distances increasing progressively such that the smallest and farthest distances differed by more than three orders of magnitude. These plots were designated sites 1–5 (Fig. 1). In each plot 8–16 replicate samples were removed by depressing a sterile plastic test tube (13-mm diameter) into the soil to remove a minimally disturbed core.

Numerous methodologies have been used to estimate abundance of algae in microbiotic soil crusts. These methods include chlorophyll *a* content (Beymer and Klopatek 1991, Klopatek in press), direct counts using fluorescence microscopy (Johansen and Rushforth 1985, Tchan 1952), dilution plate techniques (Johansen et al. 1993, Rayburn et al. 1982), and the moistened soil method (Johansen et al. 1984, 1993, St. Clair et al. 1986). All methods have advantages and disadvantages, some of which have been discussed elsewhere (Metting 1981). In this study, floristics was studied using several methodologies, while heterogeneity was examined using the dilution plate technique.

To make dilution plate cultures, the cores were returned to the laboratory. The plastic tubes were broken open such that 0.5 g of surface crust could be subsampled from each tube. These subsamples were subsequently plated on solidified Bold's Basal Medium (Bold 1949) in 10^{-1} and 10^{-2} dilutions. Viable counts of algae were made after 30 days of incubation. Although we could not enumerate by species, algal colonies were identified as either belonging to Cyanophyta or Chlorophyta/Xanthophyceae. In all cases the 10^{-1} dilution plates were used.

Site 1 contained 16 samples and was plated within one month of collection, with 3 replicate plates per sample. The other sites were plated within two months of collection, with 4 replicates per sample. Dominant algae were isolated from the dilution plates and subsequently identified using standard texts (Ettl 1978, Geitler 1930–32, Komarek and Fott 1983). Additional cyanobacteria were identified from soils moistened with Chu 10 Medium (Chu 1942). Diatoms were identified from permanent Naphrax mounts of selected soil samples (Johansen et al. 1982).

Individual sites were compared using analysis of variance (ANOVA) for an unbalanced, nested design (samples nested in sites) using the SAS GLM procedure (SAS Institute, Inc. 1985). Tukey's Honest Significant Difference (HSD) procedure was used to compare means when the ANOVA model was significant. Sites were progressively grouped to study heterogeneity of different-sized sample areas (Fig. 1). The first group (A) included samples from site 1, which were collected adjacent to each other such that samples were 0.013 m apart (the diameter of the sample tubes). The second group (B) included samples from sites 1 and 2 and represented a sample distance of 0.03 m. The third group (C) included samples from sites 1, 2, and 3 (sample distance = 1 m), the fourth group (D) included [illegible] Utah [illegible] M[illegible] [illegible]ations [illegible] plates (BBM [illegible] Chu and N[illegible]).

	BBM	Ch[illegible]	Naphrax
C[illegible]			
N[illegible] K[illegible] S[illegible]	X		
[illegible] (Desm[illegible])		X	
[illegible] (Vaucher) [illegible]		X	
[illegible] Fremy		X	
[illegible] Wille	X	X	
M[illegible] vaginatus Vaucher [illegible] Gom.		X	
N[illegible] C[illegible]	X		
N[illegible] Kuetzing	X	X	
N[illegible] (Kuetz.) H[illegible]		X	
O[illegible] Fremy		X	
O[illegible] Fremy	X	X	
P[illegible] Schroeder[illegible] Gomont	X		
P[illegible] S[illegible] & Simon	X		
S[illegible] (Ag.) Gomont		X	
S[illegible] (Kuetz.) Gomont	X	X	
S[illegible] Skuja	X	X	
S[illegible] Montagne	X		
C[illegible]			
C[illegible] Krug	X		
C[illegible] K[illegible] Fott	X		
[illegible] & [illegible]	X		
[illegible]	X		
[illegible]			X
[illegible]	X		
[illegible]		X	X
[illegible]		X	X
[illegible]			X
[illegible]			X

samples from sites 1, 2, 3, and 4 (sample distance = 12 m), and the fifth group (E) contained all samples (sample distance = 24 m).

The degree of aggregation in the algal populations of each of the above-mentioned groups was measured by determining the index of dispersion (variance-to-mean ratio; see Ludwig and Reynolds 1988). The coefficient of variation (standard deviation-to-mean ratio) was also determined for each group of samples. The random pairing technique for analysis of spatial pattern designed by Goodall (1974) was applied to the data. This technique is mathematically related to grid analysis or hierarchical analysis of variance (Goodall 1961, Greig-Smith 1952). It entails randomly selecting pairs of samples that are set distances apart until all samples are assigned to pairs. The mean variance of all pairs belonging to a distance class is computed for each class. Three randomizations were conducted with the data from this study.

RESULTS

A total of 25 taxa were observed, mostly cyanobacteria (Table 1). Most of these algae are typical soil forms, although some have not been reported in other floristic surveys of soil algae in the Great Basin and Colorado Plateau (Anderson and Rushforth 1976, Ashley et al. 1985, Johansen et al. 1981, 1982, 1984). The use of several different methods likely increased the number of taxa observed, even though we did not make enough isolations to ensure that we identified all chlorophytes and xanthophytes present.

The density of algae varied by an order of magnitude between individual samples, ranging from 7.0×10 to 9.2×10^4 cells/g dry weight soil. This is fairly homogenous compared to studies in which soils under a number of different canopy types are taken. For example, Johansen et al. (1993) found a range spanning three orders of magnitude in an undisturbed sagebrush community in Washington. However, it should be remembered that the data reported in the present study are from a single sample date rather than from multiple sample dates throughout the year as in the Washington study.

Analysis of variance revealed significant differences between the five sites, as well as significant variation between samples ($p < .001$). The Tukey multiple range test showed that site 1 had significantly greater algal density than sites 2, 3,

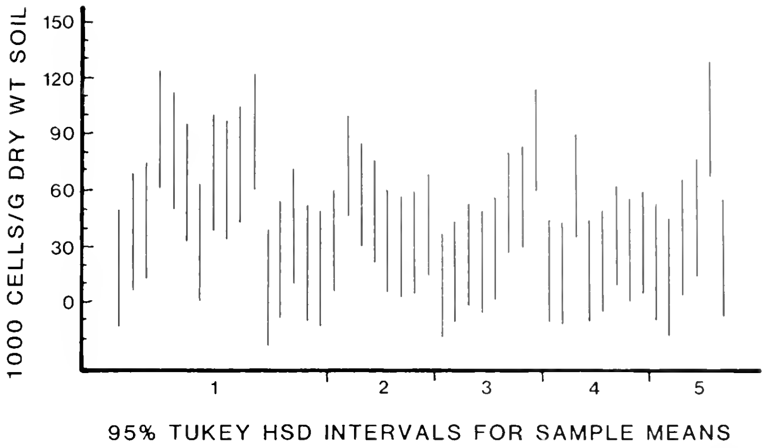


FIG. 2. Tukey Honest Significant Difference confidence intervals for counts of total algae in all samples from sites 1–5. Pairs of sample means are significantly different when their confidence intervals do not overlap.

and 4. Site 5 was not significantly different from any site. Two other ANOVAs were run, one using densities of Chlorophyta/Xanthophyceae, the other using densities of Cyanophyta. Results identical to those using total algal density were obtained.

Although there were significant differences between sites, it is difficult to consider these differences meaningful. Samples were taken from very similar sites with no visible differences. Prior small-scale impacts, such as trampling by grazing animals or defecation, may have led to the heterogeneity between sites. Runoff patterns may also have influenced crust development. The results of the Tukey multiple range test for individual samples demonstrate the variability that can exist between adjacent samples within sites (Fig. 2).

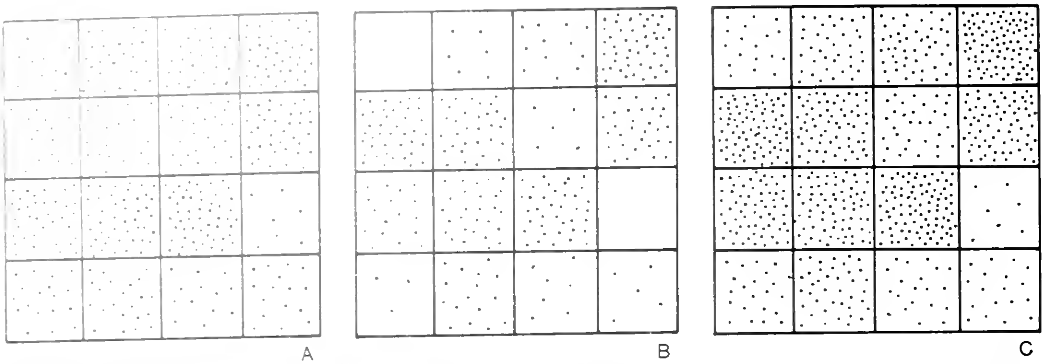
The index of dispersion (variance to mean ratio) is a measure of randomness of distribution. A value of 1.0 indicates a totally random distribution. Values much greater than 1.0 indicate aggregation. In this study, groups of all sizes (groups A–E; see Fig. 1) showed a high degree of clumping, with Cyanophyta having a more aggregated distribution than Chlorophyta and Xanthophyceae (Table 2).

The coefficient of variation (standard deviation to mean ratio) can be used to make comparisons between the amount of heterogeneity within one site and that within other sites, even though the sites may have different sample sizes and means. The larger the coefficient, the greater the degree of heterogeneity. If heterogeneity increased as the distance between samples increased, then the coefficient of variation would increase as one included samples from increasingly larger areas. Our data were surprising in that the coefficient of variation remained nearly constant for both Chlorophyta and Cyanophyta for all sample groups (Table 2). This result implies that the heterogeneity among samples 0.013 m apart (group A) was as great as that among samples taken from a transect 24 m long (group E). This indicates that soil algal patchiness can be as significant on a scale of 0.013 m as it is on a scale of 24 m (over three orders of magnitude).

TABLE 2. Index of dispersion and coefficient of variation for Chlorophyta/Xanthophyceae (CHLOR) and Cyanophyta (CYANO) for the five groups of samples.

	Index of dispersion		Coefficient of variation	
Group—Distance	CHLOR	CYANO	CHLOR	CYANO
A—0.013 m	6.4	13.6	0.46	0.86
B—0.03 m	5.2	11.4	0.43	0.78
C—1.0 m	4.8	13.7	0.43	0.88
D—12 m	4.7	13.9	0.43	0.93
E—24 m	5.2	11.2	0.45	0.95

The 16 samples comprising site 1 (group A) were collected from a four-by-four grid. By illustrating the density of organisms in thousands of cells per gram dry weight soil, we could examine aggregation patterns in a square 5.2 × 5.2



[illegible] M[illegible] [illegible] in 16 adjacent samples in site 1, group A. A, Chlorophyta and Xanthophyceae. B, [illegible] C, [illegible]

TABLE 3. Analysis of spatial pattern using Goodall's random pairing technique. Three separate analyses were run using [illegible] algae.

	First analysis		Second analysis		Third analysis	
S[illegible]	df	Variance	df	Variance	df	Variance
[illegible]	7	2[illegible]6.77	7	242.92	4	15.24
[illegible]	4	154.49	4	170.65	5	79.66
[illegible]	[illegible]	160.78	4	118.29	5	139.55
[illegible]	4	172.46	4	54.00	4	25.38
[illegible]	[illegible]	147.50	3	191.86	4	110.12

[illegible] Fig. 3). It appears that some adjacent samples had similarly high densities (five samples in the middle left, two samples in the upper right). However, grid size is too small to evaluate patchiness on this scale with confidence.

Our sampling design lent itself to analysis of spatial pattern by random pairing of samples, a method proposed by Goodall (1974) as being superior to grid analysis. Our data are dissimilar to data generally used in this type of analysis in that they were not collected at random throughout the pinyon-juniper community, but were [illegible] collected in homogeneous crusted sites [illegible] group). Thus the large-scale patterns of heterogeneity that may be associated with [illegible] vascular plant cover would not be [illegible]. We considered the analysis [illegible] it provided a completely [illegible] the question of heterogeneity [illegible] minimal [illegible] ing [illegible] ance will increase as the distance class increases until the minimal area is reached, at which point mean variance levels off or even drops with increasing distance. Two of the three random pairing analyses indicated that the minimal area for algal density in the soil crusts of our study was 0.013 m or less (Table 3). The third randomization indicated that the scale of patchiness was about 1.0 m. The third randomization may either be erroneous or suggest that the minimal area lies between 0.013 m and 1.0 m.

DISCUSSION

Most evidence from this study indicates that the minimal area for sampling soil algal crust populations is about equal to or less than 0.013 m, and that even in seemingly identical sites algal abundance can vary by more than an order of magnitude when this minimum area is used. When dissimilar sites are examined, other scales of patchiness and greater ranges of algal abundance probably would be observed. Four scales of patchiness are likely: (1) the microscale patchiness within similar sites observed in this study, (2) a small scale of patchiness that reflects the type and extent of vascular plant cover, (3) a large-scale pattern that reflects differences in disturbance levels due to grazing livestock, off-road vehicles, or rangefire, and (4) macroscale patterns due to differences in soil type, altitude, precipitation, annual temperature regimes, and type of vascular plant communities resulting from the sum of these factors.

In past studies researchers have been most interested in eliciting the two largest-scale patterns (Anderson and Rushforth 1976, Cameron 1960, Johansen and St. Clair 1986, Johansen et al. 1982, 1984, 1993). However, to accurately determine patterns on a large scale, adequate and representative samples must be taken. Consequently, an understanding of the smaller scales of patchiness is necessary before a proper sampling procedure can be selected. This study is preliminary in nature because only the smallest scale of pattern is examined. The significant differences existing between sample sites indicate that errors could easily be made in other studies because of seemingly random (or at least unexplained) microscale differences in algal abundance.

Sampling of microbiotic crusts is destructive, and so taking large samples that would lessen the problem of microscale patchiness is undesirable. Large surface soil samples are also more difficult to process and subsample. We recommend that future workers take composite samples consisting of numerous samples of similar area and depth. If the small-scale patterns of algal abundance associated with vascular plant cover are to be explored, composite samples should consist of subsamples taken at random intersections of a sampling grid placed over large quadrats. If the larger-scale patterns are under study, then it may be better to sample systematically or randomly along long transects, combining numerous small samples taken along the transect into the composite samples to be examined. Regardless of the method of quantification (chlorophyll *a*, direct counts, dilution plate counts, or moistened soil method), this type of composite sampling would be superior to taking small or large individual samples from the different areas of interest.

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MICROBIAL SPATIAL HETEROGENEITY IN MICROBIOTIC CRUSTS IN COLORADO NATIONAL MONUMENT. II. BACTERIA

Catherine Cole Wheeler[1], Valerie R. Flechtner[1,2], and Jeffrey R. Johansen[1]

ABSTRACT.—Microbial spatial heterogeneity and bacterial composition of homogeneous surface soils showing evident microbiotic crust development located under Utah juniper canopies in Colorado National Monument were studied. Four distinct homogeneous sampling sites positioned along a 12-m transect were compared on the basis of bacterial density and taxa composition.

Bacterial densities showed a range differing by several orders of magnitude. In comparisons of adjacent soil samples or samples taken from two different sampling sites within close proximity, adjacent samples showed no more similarity to each other on the basis of bacterial density or taxa composition than did more widely separated samples. The bacterial composition of these soils included members of the genera *Bacillus*, *Micrococcus*, and *Arthrobacter*. Actinomycetes were also prevalent.

Key words: bacteria, soil, cryptogamic crusts; microbiotic crusts, heterogeneity, pinyon-juniper, Colorado National Monument; actinomycetes, Micrococcus; Bacillus

Soils are complex and dynamic environments. Microorganisms influence soil fertility through their roles in the biogeochemical cycles for carbon, nitrogen, and phosphorus, and hence affect the ability of the soil to support more complex plant and animal life. These organisms, which include actinomycetes, bacteria, cyanobacteria, eukaryotic algae, fungi, and protozoa, are influenced by soil chemistry, texture, moisture, and the biotic community of which they are a part (Atlas and Bartha 1981, Dommergues et al. 1978, Focht and Martin 1979).

Desert soils, because of the limited availability of water and organic material, present a particularly challenging environment for microorganisms. Nevertheless, desert soils have been shown to contain most if not all of the major taxonomic groups represented in other soils (Focht and Martin 1979). Due to extensive heterogeneity existing in arid and semiarid soils, microbial densities reported in the literature show considerable variation in range (Skujins 1984). Bacteria, including actinomycetes, are generally the numerically dominant microorganisms (Kieft 1991). Those organisms capable of forming specialized resistant structures, such as endospores (*Bacillus*), conidia (*Actinomycetes*), capsules (*Alcaligenes*), or cysts, are generally most abundant (Chen and Alexander 1973), with gram positive bacteria usually outnumbering gram negative organisms (Atlas and Bartha 1981).

Bacteria are not uniformly distributed in soils. They are more prevalent in the organically rich parts of the soil, such as in the surface layers, areas beneath vascular plant canopy, and the rhizosphere (Atlas and Bartha 1981, Skujins 1984). Even within environments which at the macroscopic level appear to be homogeneous, microhabitats can exist (Greenwood 1961, Karl 1986), and bacterial communities inhabiting these microhabitats show significant differences in both density and composition.

The study of microbial distribution in desert and semiarid soils is minimal, and most research in this area has compared microbial density or composition between two or more habitats (Baker and Wright 1988, Cameron 1969, Skujins 1984, Vollmer et al. 1977). However, to determine the microbial differences between dissimilar habitats, one must first consider the amount of variability existing within an apparently homogeneous habitat. Most work on microbiotic crust communities of semiarid and arid lands has focused on cyanobacteria, eukaryotic algae, lichens, and mosses (Harper and

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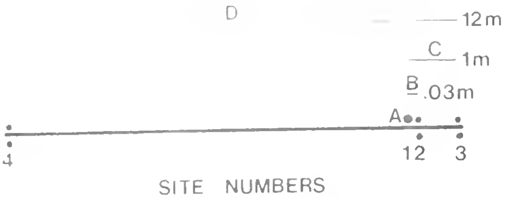

Fig. 1. Sampling area (not to scale). Sites are numbered 1–4. Groups of samples (A, B, C, D) for which the index of dispersion and the coefficient of variation were calculated (see Table [illegible]).

Marble 1988, West 1990). Bacteria (including actinomycetes) and fungi have received less attention.

Beymer and Klopatek (1991) stated that microbial heterogeneity was high in microbiotic crusts, and led to high standard errors in their study of chlorophyll *a* content of such crusts. Grondin and Johansen (1993) reported on spatial heterogeneity in algal/cyanobacterial populations of microbiotic crusts beneath Utah juniper in Colorado National Monument. As a companion study to their research, we examined the spatial heterogeneity of the heterotrophic bacterial communities in the same samples. Our work differs from past microbial investigations in that we examined the bacterial composition of microbiotic crusts covering only the surface 1 cm of soil rather than bacteria from deeper layers.

MATERIALS AND METHODS

Forty soil samples were collected in January 1989 from a pinyon-juniper woodland in Colorado National Monument, near Grand Junction, Colorado. All samples were collected from homogeneous bare soil areas showing evident cyanobacterial crust development under Utah juniper canopies. The total sampling area was divided into four distinct sampling sites, each located at a different position along a 12-m transect (Fig. 1). Sixteen adjacent samples, numbered 1.1–1.16, were collected at site 1, while eight samples numbered 2.1–2.8, 3.1–3.8, and 4.1–4.8 were collected from each of the remaining sites.

Sterile plastic centrifuge tubes ([illegible] mm in diameter) were used to remove cores of the top [illegible]. Analysis of the soil samples [illegible] the following eight-week period. [illegible] stored under refrigeration [illegible] processed at four weeks and the remaining samples at eight weeks. Subsamples of 0.5 g removed from the top 1 cm of surface soil were subsequently used to make dilutions of 10^{-1}, 10^{-2}, 10^{-3}, and 10^{-4} using sterile 0.7% NaCl buffer solution. A 0.1-ml aliquot of each dilution was inoculated onto standard nutrient agar (DIFCO) plates. Three replicates/dilution were made for samples from site 1, five for the remaining samples.

At the initiation of the study several different culture media were tried, including nutrient agar, standard plate count agar, and dilute nutrient medium. Standard nutrient agar plates gave highest numbers of CFU/g and were therefore used for all subsequent work.

Following incubation at 30°C for one week, colonies of heterotrophic bacteria on each plate were counted. Those plates yielding counts of 100–300 CFUs were used to determine the density of microorganisms (CFU/g) in each sample.

In addition to quantifying total culturable heterotrophic microorganisms per sample, samples were scored as to presence or absence of several distinctive, recognizable colony morphologies (taxa). For site 1 samples, 17 distinctive colonial types (taxa 1–17) were identified. The density of these 17 taxa (10^{-3} dilution) was recorded for samples 1.1–1.16. If a particular taxon was absent on the 10^{-3} plates but present at other dilutions, it was assigned a value of 10^3 CFU/g to indicate its presence in trace quantities.

A similar procedure was followed for sites 2, 3, and 4, with a total of 15 distinct taxa being selected for enumeration. Five of these taxa (6, 10, 11, 12, and 16) had previously been selected and scored in site 1. The remaining 10 taxa (18–27) had not been previously identified.

An attempt was made to isolate all 17 taxa enumerated in site 1. However three of the actinomycetes in this group did not grow in subculture. Thirteen additional distinctive bacterial types from site 1 were isolated for future identification. Because of time constraints, no bacteria were isolated or identified from sites 2, 3, and 4.

After the establishment of organisms in pure culture, colonial morphology, cellular morphology, motility, and physiological characteristics for each isolate were determined using standard techniques (Atlas et al. 1988; see Cole 1990 for full details). As part of this characterization, the following tests were performed: carbohydrate utilization (arabinose, glucose, mannitol, xylose),

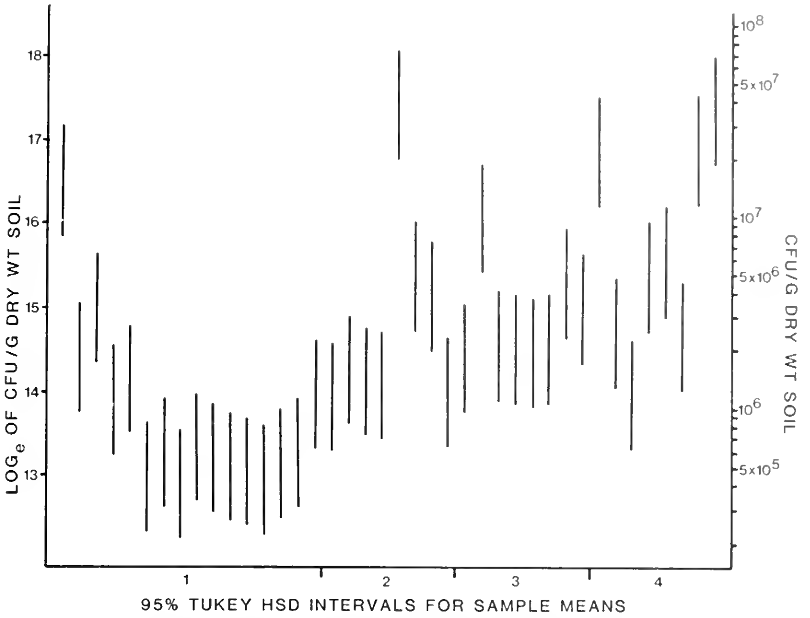

Fig. 2. Tukey HSD confidence intervals for individual samples. Data were Log$_e$ transformed before analysis of variance. Significant differences in the samples existed ($p < .0001$).

H_2S production, anaerobic growth, catalase, gelatinase, amylase, oxidase, urease, nitratase, indole production, citrate utilization, litmus milk reaction, Vogues-Proskauer (VP), methyl red (MR), growth on nutrient agar at 37°C and 50°C, growth on 7, 10, and 12% NaCl nutrient agar media, and growth on EMB and ENDO agar (Atlas et al. 1988). Following characterization, identification of unknowns was attempted using Bergey's Manual (Krieg and Holt 1984, Sneath et al. 1986).

Individual samples and sites were compared using analysis of variance (ANOVA) on Log$_e$ transformed data. Tukey's (HSD) procedure was used to compare means when the ANOVA model was significant. A box and whisker plot was constructed for site data. This plot divides the data into four areas of equal frequency. The box encloses the middle 50%, with the horizontal line representing the median. Whiskers extend to the nearest point within 1.5 interquartile ranges from the box, with points lying outside this range being plotted as individual outliers (STSC 1991).

Sites were progressively grouped to study heterogeneity of different-sized sample areas (Fig. 1). The first group (A) included samples from site 1, which were collected adjacent to each other such that samples were 0.013 m apart (the diameter of the sample tubes). The second group (B) included samples from sites 1 and 2 and represented a sample distance of 0.03 m. The third group (C) included samples 1, 2, and 3 (sample distance 1 m), and the fourth group (D) included samples from sites 1, 2, 3, and 4 (sample distance 12 m). The samples, sites, and groups of samples used in this study were identical to those used by Grondin and Johansen (1993).

The degree of aggregation in the bacterial populations of each of the above-mentioned groups was measured by determining the index of dispersion (variance-to-mean ratio; see Ludwig and Reynolds 1988). The coefficient of variation (standard deviation-to-mean ratio) was also determined for each group of samples. The random pairing technique for analysis of spatial pattern designed by Goodall (1974) was applied to the data.

RESULTS

Within the 40 samples analyzed, bacterial density (culturable heterotrophs) ranged from 4.0×10^5 to 3.8×10^7 CFU/g dry weight soil. This range of density is consistent with values reported in the literature for similar desert soil habitats (Cameron 1969, Skujins 1984). Analysis

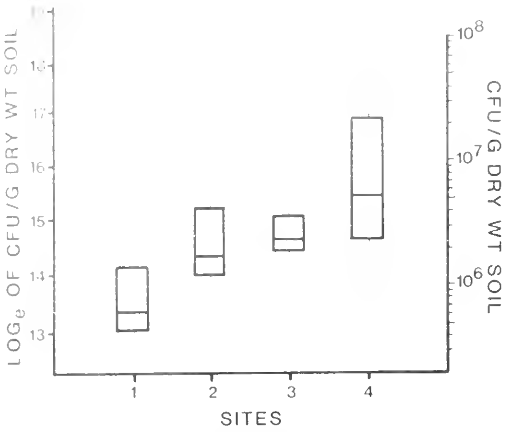

Fig. 3. Box and whisker plot for the four sites. Data were Log$_e$ transformed before analysis of variance. Significant differences in the sites existed ($p < .0001$). Tukey's HSD procedure indicated that only the means of sites 1 and 4 were significantly different.

of variance combined with Tukey's multiple range test demonstrated significant variability within the data both between samples (Fig. 2) and between sites (Fig. 3). Sites 2, 3, and 4 had similar ranges and roughly similar means. Site 1 had lower minimum and maximum densities, as well as a lower overall mean. Only sites 1 and 4 had significantly different means. It is interesting to note that sites 2 and 3 are more similar to the distant site 4 than they are to the closer site 1 (Fig. 1).

Within sites, variability between proximal replicate samples was very high. For example, the density of organisms in sample 1.1 was 1.5 × 10 CFU/g, while adjacent sample 1.5 had only 1.4 × 10 CFU/g; sample 2.5 contained 3.7 × 10 CFU/g, while adjacent sample 2.1 contained 1.2 × 10 CFU/g. Similar examples can be found in all four sites (Cole 1990).

The index of dispersion is a measure of patchiness. A value of 1.0 indicates a totally random distribution. Values greater than 1.0 indicate aggregation. For groups of all sizes (A–D) the index of dispersion was much greater than 1.0 (Table 1), indicating that bacteria clearly had an aggregated distribution at all distances represented. This pattern is similar to that seen for algae (prokaryotic and eukaryotic) from the same groups of samples (Grondin and Johansen 1993).

Although the index of dispersion demonstrated patchiness within all sample groups, it did not reveal the scale of patchiness. The coefficient of variation can be used to make comparisons between the amount of heterogeneity within one site and that within other sites, even though the sites may have different sample sizes and means. The higher the coefficient, the higher the degree of heterogeneity. If heterogeneity increased as one sampled further and further apart, then the coefficient of variation would increase as one included samples from increasingly larger areas.

Table 1. Index of dispersion, coefficient of variation, and mean cell density for bacteria for the four groups of samples.

Group–Distance	Index of dispersion	Coefficient of variation	Mean CFU per gram
A–0.013 m	7,200	200	1.8×10^6
B–0.03 m	18,000	230	3.4×10^6
C–1.0 m	13,700	200	3.5×10^6
D–12 m	15,900	180	5.2×10^6

The coefficient of variation for the four groups of samples, representing distances of 0.013 m, 0.03 m, 1.0 m, and 12 m, differed by less than 24%, indicating that heterogeneity at 0.013 m was roughly similar to that at 12 m (Table 1). This suggests that the patchiness of soil microorganisms may be as significant on a scale of less than 0.013 m as it is on a scale of 12 m. However, the maximum coefficient of variation was seen at 0.03 m, and it may be that patches of this size were important. Thus, the results of this analysis were not as unequivocal as those presented for the algal populations at the same site (Grondin and Johansen 1993).

The distribution of microorganisms differed between samples not only in terms of absolute density but also in terms of specific taxa. Thus, heterogeneity exists on both quantitative and floristic levels. Floristic analysis was most thorough for site 1. The spatial distribution of individual taxa throughout this site was evident. Several of the taxa (1, 3, 4, 8, 16, and 17—mostly actinomycetes) were distributed in only a few of the samples, while others (2, 5, 6, 7, 11, 12, 13—mostly *Bacillus* and *Micrococcus*) were present in most samples (Table 2). In fact, more than 50% of the taxa were present in more than 50% of the samples. When individual taxa densities were considered, the heterogeneity between proximal samples was even more striking than the differences in total density. For example, taxon 1 was present in sample 1.1 at a

TABLE 2. Average relative densities for each of the 17 taxa scored in 16 samples from site 1.

	Sample															
Taxon	1.1	1.2	1.3	1.4	1.5	1.6	1.7	1.8	1.9	1.10	1.11	1.12	1.13	1.14	1.15	1.16
1	99.5			0.4									1.2			
2				16.7	25.7	5.9	2.5	8.0	20.7	9.7	3.1	5.4	1.2	8.7	24.6	17.8
3		6.9	37.3													
4										2.2	1.0	17.9				1.8
5	0.5	16.0	30.3	1.3	1.8	10.9	8.3	4.3	2.1	5.2	27.6	12.5	8.6	20.5	2.5	
6		9.0	9.9	2.9	19.8	42.0	52.1	37.0	11.7	27.6	27.6	17.9	33.3	13.2	24.6	21.9
7		32.6	9.2	7.1	1.8	14.3	16.5	14.2	6.9	14.9	13.3	17.9	3.7	6.8	10.7	
8				65.7	0.6			0.6								
9						2.5			4.8	0.7			1.2		0.8	
10		6.9	4.9	1.3	16.2	0.8	0.8	1.9	0.6	5.2	3.1	5.4		8.9	5.7	4.4
11		27.8	12.0	4.2	6.0	10.9	5.8	29.0	9.0	7.5		12.5	21.0	6.8	2.5	23.7
12			0.7		16.2	0.8	2.5	4.3	29.6	12.7	1.0	1.8	16.0	6.8	5.7	0.6
13		0.7	0.7	0.4	7.8	8.4	5.8	0.6	9.0	12.7	7.1	1.8	3.7	0.7	8.2	1.8
14						2.5	5.8					5.4	1.2	2.1	0.8	0.6
15					4.2	0.8			4.8	0.7	3.1	1.8	8.6	0.7	10.7	5.9
16									0.6					0.7	0.8	21.9
17										0.7	13.3			2.1	2.5	

density of 1.3 × 10^7 cells/g, while in samples 1.4 and 1.13 it was present at a concentration of 1.0 × 10^3 cells/g, a difference of four orders of magnitude.

The distribution of the 15 taxa scored in the remaining sites showed variability similar to that scored in site 1 (Table 3). Some of the taxa scored from sites 2, 3, and 4 (6, 10, 11, 12, and 16—mostly *Micrococcus*) had been scored in site 1 as well, though most were distinctly different from those scored in the previous month. Taxa 6, 10, 11, and 12 were well distributed throughout all four sites. This indicates that although sampling sites 1 and 4 were separated by a distance of 12 m, there was some degree of similarity in terms of types of microorganisms present. Many of the taxa (e.g., 18, 19, 20, and 26) were widely distributed throughout sites 2, 3, and 4, indicating additional similarity between these sites. Some taxa (such as 12, 21, 22, 27) were restricted to only a few sampling sites.

As observed in site 1, more than 50% of the taxa were represented in more than 50% of the samples of sites 2, 3, and 4. Likewise, the density of several taxa varied markedly from sample to sample. Taxon 16 was present in six of the eight site 4 samples, ranging from a density of less than 1 cell/mg (4.4) to a density of 1840 cells/mg (4.1).

Some taxa were uniformly high in density in the samples in which they were present. Taxon 18, present in 21 of 24 samples, had a relative density greater than 40% in 10 of those samples (Table 3). On the other hand, some taxa were very uneven in their density, an example being taxon 25, which had a relative density of less than 0.1% in some samples and 100% in others.

Although the identification of bacteria to the species level was not a major goal of this work, some effort was made to do a preliminary characterization of the types of bacteria present in site 1 (Table 4). As expected, the majority of the isolates were gram positive bacteria, including actinomycetes. Five individual isolates of the genus *Bacillus* were recovered, with two being identified to the species level (*B. subtilis* and *B. licheniformis*). Seven isolates of *Micrococcus* were recovered, with only one (*M. kristinae*) being identified to species. Of seven actinomycetes, only one could be identified to genus level (*Streptomyces*). Of four non-spore-forming gram positive rods, one was identified as belonging to *Arthrobacter*. The four gram negative rods could not be identified even to genus level.

DISCUSSION

Our purpose in this study was to compare spatial heterogeneity of heterotrophic bacteria and actinomycete populations in the surface crust of apparently homogeneous soils. No effort was made to completely characterize the bacterial community nor to isolate all taxa present. Since we were interested in a comparative [illegible] in 24 samples from [illegible] and 4

	Sample																							
[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	27	28	31	32	33	34	35	36	37	38	41	42	[illegible]	[illegible]	[illegible]	[illegible]		
[illegible]	[illegible]						[illegible]	[illegible]	[illegible]		5.6	[illegible]		27.7	10.5	6.1			0.1			[illegible]		
[illegible]	[illegible]					[illegible]	[illegible]	[illegible]						9.2	1.8	0.1	1.7	2.8	[illegible]			[illegible]		
[illegible]	[illegible]					0.1	18.5		0.1		0.1			26.2	3.5	6.1	0.1	1.1				[illegible]		
[illegible]								0.1			0.1	3.3		3.1	8.8	3.2								
[illegible]				0.1	[illegible]		27.7	2.6	0.1	17.4	0.1	3.3	6.7	3.1		0.1	77.3	52.1	9.1		95.8	[illegible]	[illegible]	[illegible]
		[illegible]	[illegible]	[illegible]		2.0	18.5	42.1	50.0	10.9	50.0	53.3	46.7	21.5	47.4	38.7	16.0	7.0	75.8	29.2	2.1	[illegible]		
	[illegible]	[illegible]	[illegible]	17.4		0.5	4.6	5.3	14.3		30.6	10.0		7.7	28.1	12.9		0.1	0.1					
[illegible]	[illegible]			0.1			0.1	0.1	0.1	34.8	2.7	20.0	10.0	0.1	0.1	0.1	2.5	1.4	0.1	70.8	0.1	0.1	0.1	99.9
[illegible]			0.1			97.0	15.4	7.9											9.1			39.1		
22										0.1														
23		6.2	5.0	0.1		0.1	0.1	0.1			2.7			1.5		9.7					2.1	4.4		
24	28.0			4.4				23.7	0.1		5.6							0.1	3.0			1.4		
25		0.1		0.1		0.1			0.1	0.1	0.1				0.1	0.1	2.5	0.1	0.1	0.1	0.1	0.1	99.8	
26		18.8		8.7			12.3	7.9		37.0	2.7	6.7	6.7			22.6		33.8	3.0			4.4		
27										0.1			0.1					1.4				0.1		

TABLE 4. Species identified from site 1. These isolates include several taxa in Table 2, which are indicated here with a taxon number. Some characteristics of the bacteria are given. For full characterization see Cole (1990).

Species	Taxon	Color[1]	Arrangement[2]	Acid	Motility
Bacillus subtilis (Ehr.) Cohn	5	B	S,PR	[illegible]	[illegible]
Bacillus licheniformis (Weigm.) Ches.		None	S,PR	[illegible]	
Bacillus sp. 1	7	None	S,PR,CH		
Bacillus sp. 2		None	S,PR		
Bacillus sp. 3		None	S,PR		[illegible]
Micrococcus kristinae Kloos et al.	9	PO	T	[illegible]	
Micrococcus sp. 1	11	BY	T	[illegible]	
Micrococcus sp. 2		BY	T	[illegible]	
Micrococcus sp. 3	13	PR	T		
Micrococcus sp. 4	12	R	T		
Micrococcus sp. 5	10	PY	T	[illegible]	
Micrococcus sp. 6		P	CL		
Actinomycete sp. 1		None	F		
Actinomycete sp. 2		None	F		
Actinomycete sp. 3	16	None	F		
Actinomycete sp. 4	17	None	F		
Actinomycete sp. 5		None	F		
Actinomycete sp. 6	2	None	F		
Streptomyces sp. 1		I	F		
Arthrobacter sp. 1		None	S		
Gram positive rods (3 isolates)	3	None	S		
Gram negative rod sp. 1	14	PK	S,PR		
Gram negative rod sp. 2		P	S,PR,CL		
Gram negative rod sp. 3		O	S,PR		[illegible]
Gram negative rod sp. 4		TO	S		

[1] Pigment: B = brown, BY = buttercup yellow, I = indigo, O = orange, P = peach, PK = pink, PO = pale orange, PR = pale red, PY = [illegible], TO = translucent orange.
[2] Arrangement: S = singles, PR = pairs, T = tetrads, CL = clusters, CH = chains, F = branching filaments.
Acid from glucose fermentation.

study, we concentrated on a subset of the bacterial community: those organisms that would grow on plate count agar at 30°C under aerobic conditions.

There was considerable heterogeneity in bacterial density and composition when samples taken within the same site were compared. This within-site heterogeneity appeared to be about equal to that observed between sites. These findings suggest that the minimal area, defined as the smallest sample possible that is still representative of the population as a whole, is likely less than 0.013 m, the smallest sample size used in this study.

The interpretation of the bacterial data was not as certain as the interpretation of the algal data for the same site (Grondin and Johansen 1993). The maximum coefficient of variation was seen at 0.03 m rather than the 0.013 m as in the algal study. However, the difference between the coefficients of variation for 0.03 m and 0.013 m was only 14%, which likely represents an unimportant difference. Goodall's random pairing technique was also inconclusive, probably due to the high density values in site 4.

It was surprising to see that site 1 had the lowest bacterial densities, since the samples from this site were processed a month before the samples from the other three sites. It is possible that some bacterial growth occurred in site 2–4 samples, even though they were stored under refrigeration. The algal populations cultured from the same dilution tubes were greatest at site 1 (Grondin and Johansen 1993), which suggests that dilution or aliquot error cannot account for the differences. We suspect that the statistically significant differences between sites observed in both the algal and bacterial studies are unimportant and probably represent random variation between sites.

Accurate determination of microbial populations in soil samples is a difficult task. James and Sutherland (1939) systematically studied experimental error associated with estimating bacterial and fungal densities in agricultural soil. They identified two main sources of experimental variance: variability between 25-g aliquots of a single sieved and mixed soil sample, and variability between replicate dilutions of single aliquots. Variation between replicate plates of a [illegible] systematic error associated with the [illegible] in which plates were prepared and incubated were less important. The authors attribute the variability between replicate dilutions to error in pipet accuracy and dilution blank preparation, as well as to the rapid settling of soil in the first dilution. These factors are probably less important in our study because of improved manufacture of scientific glassware and because we reduced settling by using a Pipetaid (Drummond Scientific) to mix dilutions. However, James and Sutherland's (1939) observation that aliquots of a single sample can differ significantly is relevant to our results.

In James and Sutherland's study of agricultural soil (which would be much richer in organics than desert soil), microscale clumping of bacterial populations was likely responsible for much of the variation they observed between aliquots. Even though the samples were screened and mixed, small water-stable aggregates were probably still present. These aggregates contain root fragments, humus, and clay and have markedly different bacterial populations than nonaggregated silt and sand. It is conceivable that some of their dilution error was also due to very small aggregates.

Our samples were 50 times smaller than the aliquots of James and Sutherland (1939). The differences between our samples likely represent the same type of microscale patchiness suggested by the variance observed in the earlier study. Another factor that gives rise to marked differences between samples is the presence of actinomycete filaments, which fragment to produce numerous propagules. Since James and Sutherland (1939) made no distinction between types of bacteria observed, it is not possible to evaluate the relative importance of actinomycete fragmentation to the variability they observed. However, we did observe samples that were dominated by a single actinomycete [illegible]. An additional factor that [illegible] microscale patchiness in our study of [illegible] the patchiness of the algal populations, which represent a major source of carbon for heterotrophic bacteria (Beymer and Klopatek 1991).

[illegible] studies at this western Colorado [illegible] several suggestions for [illegible] microbial populations [illegible]. First, taking a large sample [illegible] small aliquot is taken for [illegible] yield accurate results. It is probably better to take a number of small samples from several areas and then analyze them individually to give a composite picture of the site. Alternatively, if time and resources prohibit such a thorough approach, we recommend that multiple small samples still be taken, but that these be pooled to produce a limited number of samples. For example, one could take 15 small samples and pool them to make 3 larger samples composed of 5 samples each. This pooled approach is similar to recommendations by Grondin and Johansen (1993) for algal sampling in desert soils. Small samples are also desirable because they are less damaging to the microbiotic crust and permit repeat sampling at the same site.

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SOIL MICROSTRUCTURE IN SOILS OF THE COLORADO PLATEAU: THE ROLE OF THE CYANOBACTERIUM *MICROCOLEUS VAGINATUS*

Jayne Belnap[1] and John S. Gardner[2]

ABSTRACT.—The role of the cyanobacterium *Microcoleus vaginatus* in cold-desert soil crusts is investigated using scanning electron microscopy. Crusts from sandstone-, limestone-, and gypsum-derived soils are examined. When dry, polysaccharide sheath material from this cyanobacterium can be seen winding through and across all three types of soil surfaces, attaching to and binding soil particles together. When wet, sheaths and living filaments can be seen absorbing water, swelling and covering soil surfaces even more extensively. Addition of negatively charged material, found both as sheath material and attached clay particles, may affect cation exchange capacity of these soils as well. As a result of these observations, we propose that the presence of this cyanobacterium may significantly enhance soil stability, moisture retention, and fertility of cold-desert soils.

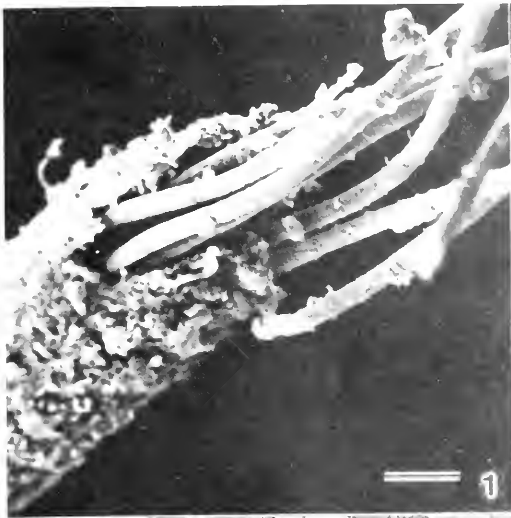
Key words: Microcoleus vaginatus, *cyanobacteria, cryptobiotic crusts, cryptogamic crusts, soil, soil microstructure.*

It has long been reported that cyanobacterial soil crusts enhance soil stability (Anderson, Harper, and Holmgren 1982, Anderson, Harper, and Rushforth 1982, Fletcher and Martin 1948, Harper and Marble 1988, Kleiner and Harper 1972, 1977, Loope and Gifford 1972). Anantani and Marathe (1974), Anderson and Rushforth (1976), Campbell (1979), and Shields and Durrell (1964) all suggest that a network of cyanobacterial filaments binds soil particles together, immobilizing them and thus enhancing soil stability against both wind and water erosion. It has also been shown that these crusts enhance moisture and nutrient retention in sandy soils (Brock 1975, Brotherson and Rushforth 1983, Campbell 1979, Harper and Belnap unpublished data, Shields and Durrell 1964).

On the Colorado Plateau, a biogeographical province that includes southwestern and eastern Utah, northern Arizona, western Colorado and northwestern New Mexico, cyanobacterial-lichen soil crusts often provide up to 70% of the living cover (Belnap 1990a). In these areas the cyanobacterium *Microcoleus vaginatus* (Vauch.) Gom. is the major constituent (Anderson and Rushforth 1976, Campbell et al. 1989), often representing up to 95% of the biomass of the soil in interspaces between vascular plants (Belnap personal observation). This is true for all substrates examined in this biogeographical province, including soils derived from sandstone, gypsum, limestone, and shale parent material, although the degree of development of the cyanobacterial-lichen crust may vary among substrates.

Since *Microcoleus* is so prevalent in these soil systems, this study examines the influence of this species on the structure and function of soil crusts on various soil types. In particular, the possible contribution of this organism to stability of arid land soils is examined.

[illegible] *M. vaginatus* in sandy soils: 1, note the large extracellular sheath surrounding the [illegible] *M. vaginatus* filaments (note the cell walls along each filament [bar = 5µm]); 3, [illegible] sheath material secreted along exposed filament (note partially exposed filament [bar = [illegible] encapsulated in a polysaccharide material (arrow indicates encapsulated filament [illegible] (arrow indicates cavity [bar = 5µm]); 6, sheaths may contain many cavities [illegible]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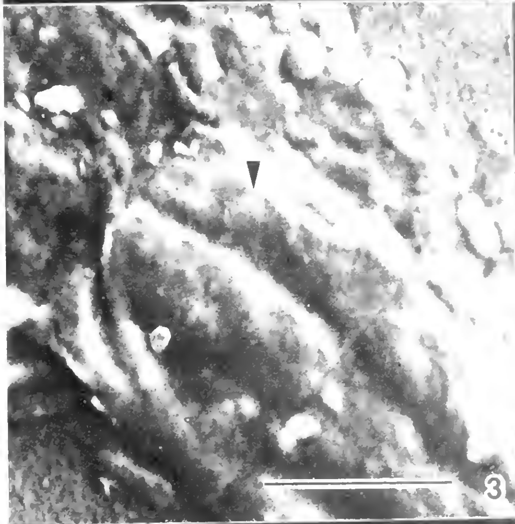
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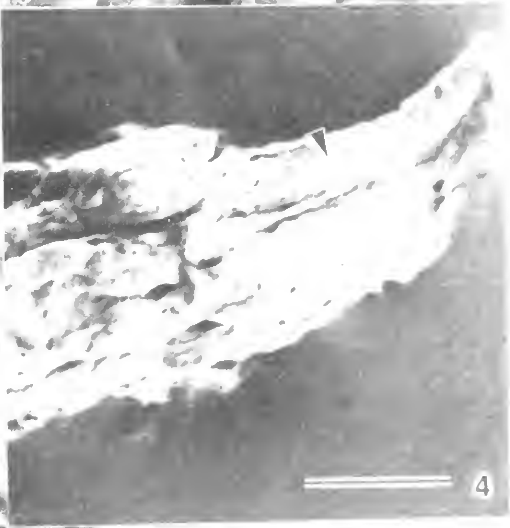
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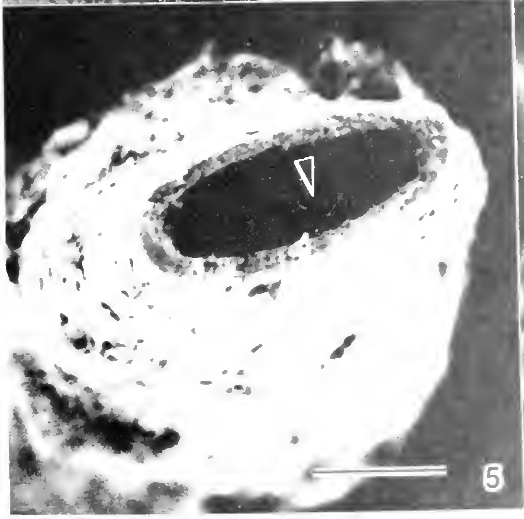
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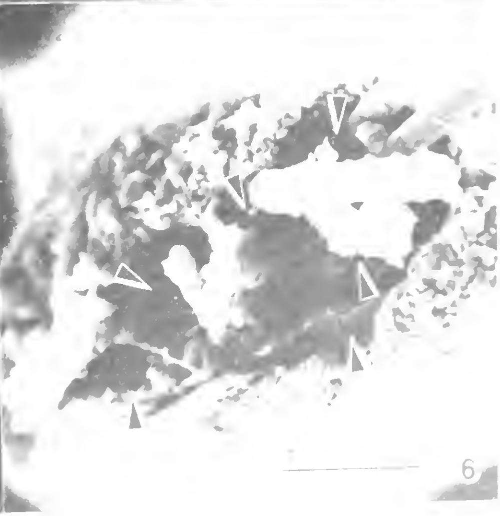
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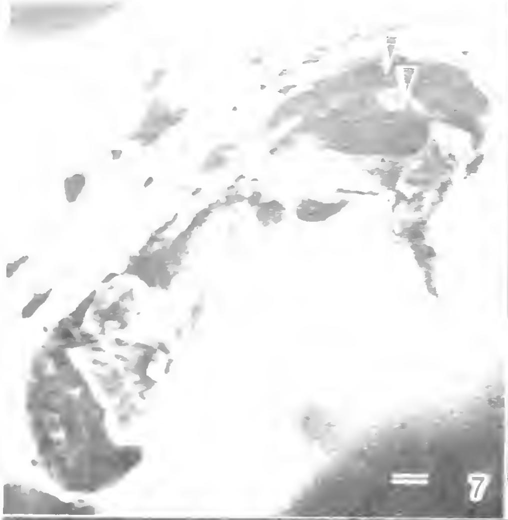

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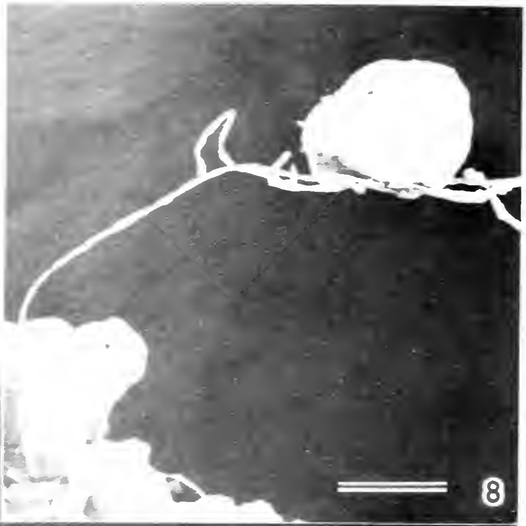

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MATERIALS AND METHODS

Cyanobacterial soil crusts were collected from three different substrate types on the Colorado Plateau in early fall. Crusts from sandstone- and gypsum-derived soils were collected from Arches National Park in southeastern Utah near Moab. Crusts from limestone-derived soils were collected from Bryce Canyon National Park in southwestern Utah near Panguitch. All crusts were transported to the lab, where they were prepared for observation using scanning electron microscopy (SEM). Two types of preparation were used: samples were either directly gold-coated and examined with a JEOL 840A scanning electron microscope or were prepared by freeze-substitution (Ichikawa et al. 1989), gold-coated, and then examined with SEM.

The presence of chlorophyll *a* was used to estimate the depth and distribution of living cyanobacteria and green algae in the crusts found on the sandy and gypsiferous soils from Arches National Park. Two-centimeter-deep cores of the crust were cut in 2-mm segments, beginning at the soil surface. Chlorophyll *a* was extracted from samples with dimethyl sulfoxide (DMSO). The DMSO extraction samples were centrifuged and spectrally analyzed on a diode array spectrophotometer (Belnap 1990b) at 665 nm to obtain relative values for the amount of chlorophyll *a* present.

RESULTS AND DISCUSSION

Microcoleus vaginatus and *M. vaginatus*-dominated crusts from sandstone-derived soils are shown in Figures 1–13. A large and distinct polysaccharide sheath surrounds groups of living filaments of *M. vaginatus* (Fig. 1). Close examination shows cellular divisions in the cyanobacterial filaments (Fig. 2). When wet, the polysaccharide sheaths swell and the filaments within are mechanically extruded from the sheath and through or across the soil surface. As the surface dries, the filaments retract somewhat into the sheath. Exposed portions of the filaments then secrete additional polysaccharide material (Fig. 3). When dry, the cyanobacterial filaments are completely encased in the polysaccharide sheaths (Fig. 4). The interior of the sheath of *M. vaginatus* may contain from one (Fig. 5) to many cavities (Fig. 6). The sheath itself can be formed by more than one secretion event (Fig. 7).

The strength of this sheath material can be seen in Figure 8, where a single strand of sheath material holds a sand grain aloft above the supporting surface. The binding effect of these cyanobacterial sheaths on sandy soil surfaces is illustrated in Figure 9. Sheaths of *M. vaginatus* wind among the sand particles, connecting individual grains, much like fibers in fiberglass. Although the sheath material is dry, it can be seen still firmly adhering to the soil particles. Secure and extensive connections to the sand grains by the sheath material are shown in Figures 10 and 11. Multiple sheaths can often be seen attached to the same sand grain, as shown in Figure 10. In Figure 11 the intimate association between sand grain and polysaccharide material can be seen.

When wet, the polysaccharide sheath material swells and covers the soil surface even more extensively than when dry. Sheath material can absorb up to eight times its weight in water almost instantaneously; thus, it absorbs precipitation quickly and increases the water-holding capacity of sandy soils (Brock 1975, Cameron and Blank 1966, Campbell 1979, 1989). Sheaths and filaments become swollen and round, forming a net over the surface of the sand (Fig. 12). Even when swollen, however, there is still space for rainwater and vascular plant roots to penetrate into the soil between sheaths.

The presence of cyanobacterial soil crusts has been demonstrated to increase the availability of many nutrients in sandy soils. Levels of N, P, K, Fe, Ca, and Mg were higher in the annual grass *Festuca octoflora* growing on crusted soils than in plants growing on comparable noncrusted soils (Belnap and Harper unpublished data). Essential nutrient concentrations were also shown to be higher in the tissue of the perennial plant *Lepidium* [illegible] growing on soils covered by cyanobacterial-lichen crusts than on paired plots where the surface [illegible] of crust had been stripped from around the plants three

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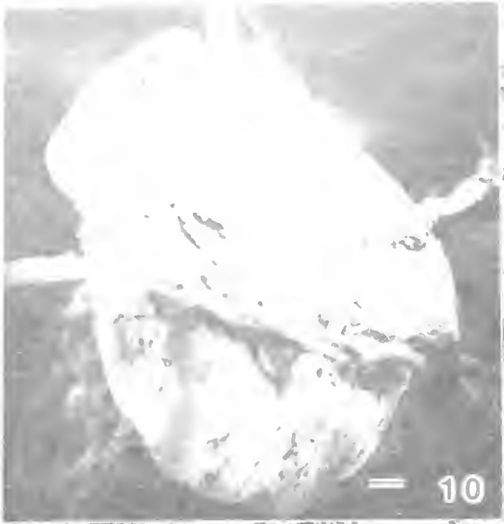
Figs. 7–9 (facing page). *Microcoleus* [illegible] in sandy soils: [illegible] arrow indicates two discrete layers of polysaccharides [illegible] note single sheath holding a sand grain aloft (bar = 100µm) [illegible] binds sand grains together [illegible] are wound around and among the sand grains (bar = 100µm).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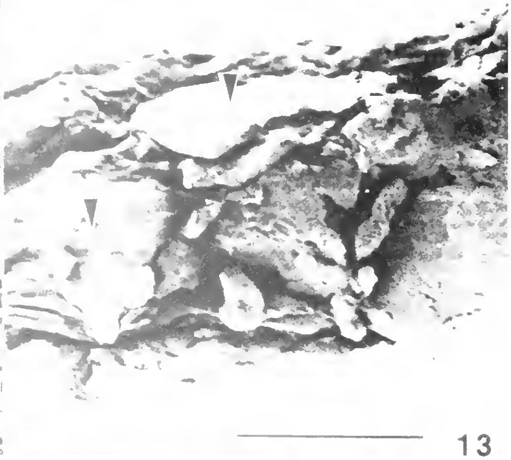
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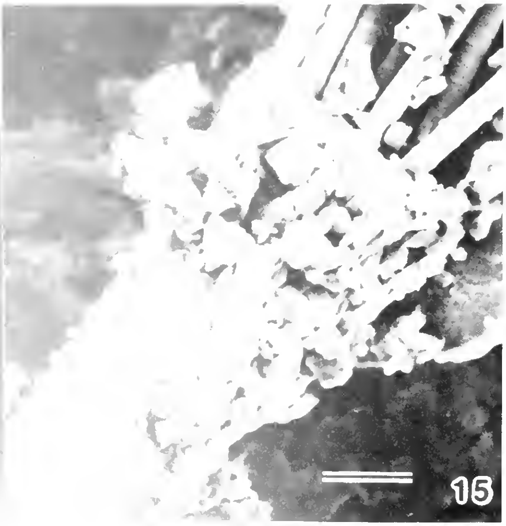
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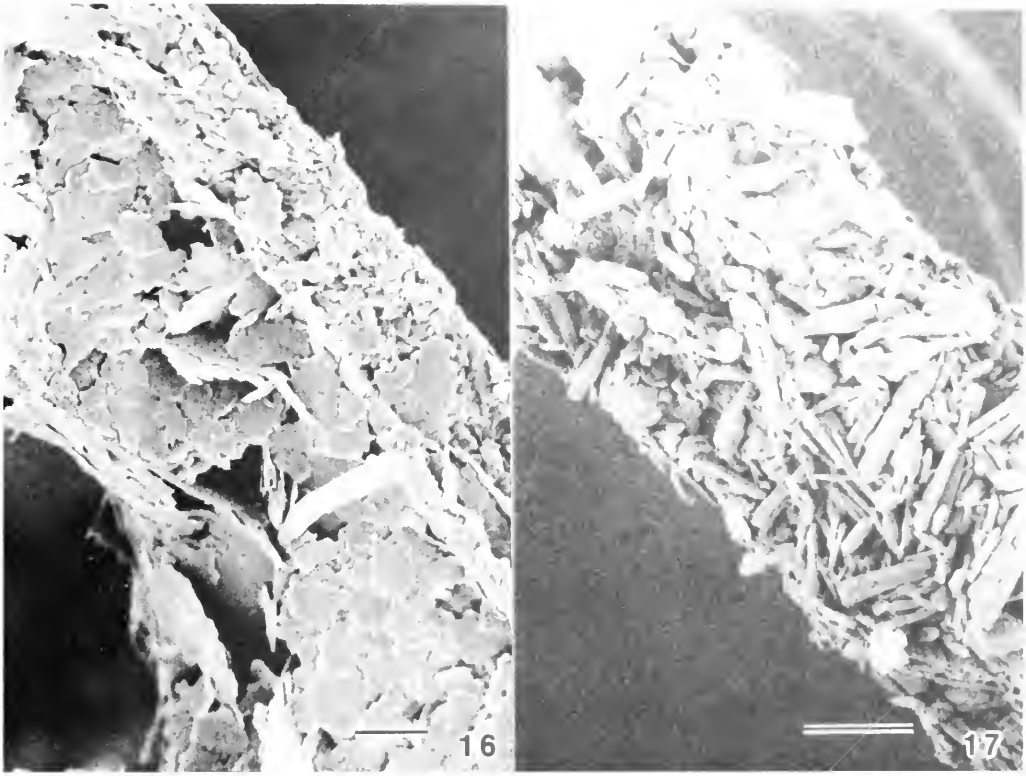

Figs. 16–17. *Microcoleus vaginatus* in gypsiferous soils: 16, sheaths in gypsiferous soils can be made of both organic and inorganic material (bar = 10µm); 17, sheaths in gypsiferous soils are often coated with gypsum crystals (note the gypsum crystals on the sheath surface [bar = 5µm]).

months prior to tissue nutrient analyses (Harper and Marble unpublished). One possible mechanism by which the cyanobacteria alters mineral availability in supporting soils is suggested in Figure 13: clay particles can be seen bound to, and incorporated into, the polysaccharide sheath material. Consequently, positively charged macronutrients bound to these negatively charged clay particles and to the negatively charged sheath material would be held in the upper soil horizons and in a form readily available to vascular plants, instead of being leached away by percolation water or bound in a chemically unavailable form.

Chlorophyll *a* distribution in the soil shows that cyanobacterial cells are probably concentrated in the top 4 mm of sandy soils, but some chlorophyll *a* is found as deep as 1 cm. Measurements of the bumpy surface topography of undisturbed crusts show that few bumps are greater than 8 mm across. Analysis shows that cyanobacterial filaments ramify throughout such surface irregularities. The volume of cyanobacterial filaments per unit soil surface coverage is thus increased greatly in areas where microtopography of the soil surface is very complex.

Figs. 10–15 (facing page). *Microcoleus vaginatus*: 10, 11, sheaths adhere firmly to sand grain surfaces (note the intimate connection between the sheath and grain surfaces [bars = 10µm]); 12, when wet, sheaths and filaments swell, covering the soil surface (note the mass of entangled sheaths covering the sand grains [bars = 100µm]); 13, clay particles (arrows) may be incorporated into sheath material (bar = 10µm); 14, in fine-textured soils such as this limestone-derived substrate, many small particles adhere to the sheath material (bar = 10µm); 15, sheath surface texture in fine-textured soils is much smoother than that in coarse-grained soils (note smooth material at the base of the sheath, which appears similar to the surrounding inorganic material [bar = 10µm]).

[illegible] the cohesion [illegible] crusts, since the [illegible] and easily crushed [illegible] 1989, Harper and Marble 1988, [illegible] 1982). Visual examination of undisturbed soil crusts on sandy soils of the Colorado Plateau shows cyanobacterial sheath material occurring as deep as 10 cm below the surface of the soil. Heavily trampled areas support only a thin veneer of cyanobacterial sheaths (Belnap unpublished data). Since no chlorophyll *a* is found below 1 cm, sheath material below that depth must represent remnants of cyanobacterial crusts once found near or at the soil surface and later buried by sediments. Though no longer associated with living filaments, such sheath material is still capable of binding soil particles together and still increases nutrient and moisture retention of associated soil. However, any damage to such abandoned sheath material is non-repairable, since living cyanobacteria are apparently no longer present at these depths to regenerate filament and sheath materials. As a consequence, trampling may not only reduce soil stability, but soil fertility and soil moisture retention as well.

In finer-textured soils the sheaths of *M. vaginatus* assume a different appearance. In such soils fine particles adhere to the outside of most sheaths, as can be seen in sheaths from a limestone-derived soil (Fig. 14). Also, the sheath surface appears much smoother in these limestone-derived soils (Fig. 15) and is much harder to the touch. It may be that water-soluble matter in these soils goes into solution when the soil is thoroughly wetted by rain. Such periods would also coincide with the time of maximum activity for the cyanobacteria. Under such conditions, [illegible] of polysaccharide material could be [illegible] with the soil particles and ma[illegible] [illegible] and, upon drying, form [illegible] part organic and part inorganic. [illegible] illustration of cyano[illegible] both organic and inorganic [illegible] the sheaths of *M.* [illegible] soil (Figs. 16, 17). [illegible] than car[illegible] dissolve when [illegible] surface of [illegible] to mix with solubilized soil materials may render sheaths less vulnerable to physical breakage.

In combination these SEM micrographs demonstrate that cyanobacterial soil crusts strongly alter the microstructure of soils in cold-desert ecosystems. The interwoven filaments of *M. vaginatus* and other filamentous cyanobacteria undoubtedly enhance soil surface stability in such environments. When undisturbed for long periods, cyanobacterial sheaths may be found at depths as great as 10 cm below the surface of sandy soil. Thus, as aeolian and water-borne materials are trapped in the polysaccharide sheaths of *M. vaginatus* and other cyanobacteria growing on the surface of desert soils, these sheaths are gradually buried, but their ameliorating influences on water-holding capacity, cation exchange capacity, and soil stability may extend far below the depth to which light can penetrate.

ACKNOWLEDGMENTS

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CRYPTOGAMS, VASCULAR PLANTS, AND SOIL HYDROLOGICAL RELATIONS: SOME PRELIMINARY RESULTS FROM THE SEMIARID WOODLANDS OF EASTERN AUSTRALIA

D. J. Eldridge[1]

[illegible] Grazed and ungrazed sites were examined in a semiarid woodland in eastern Australia to determine [illegible] various types of cryptogams, and the role of cryptogams in pasture dynamics, infiltration, and water [illegible] relationships were found between vascular plant cover and cover of cryptogams for nine rangeland sites [illegible] 18-month period. In the absence of vascular plants, sites with low cover of cryptogams were dominated by algae. [illegible] presence of a cryptogamic crust had no significant effect on infiltration at ungrazed sites but significantly increased [illegible] some grazed sites. Splash erosion was very low on soils with at least 50% cryptogam cover. Below this level [illegible] increased markedly, along with the proportion of fine sediments lost.

Key words: cryptogamic crusts, hydrology, soil, infiltration, cryptogam dynamics, microphytic crusts, semiarid wood-lands, [illegible] Australia.

Cryptogamic or microphytic soil crusts are an important component of arid and semiarid rangeland environments. They occur as assemblages of algae, lichens, liverworts, and mosses and, in some areas where vascular plants are absent, are the predominant biological ground cover. In these environments cryptogams play an important role in soil stability, nitrogen fixation, and biomass production (Isichei 1990).

Cryptogams are commonly pioneering species in the revegetation of degraded soils (Bailey et al. 1973). Observations in some areas in semiarid eastern Australia suggest that cyanobacteria are the most common taxa found on disturbed sites. The relationship between vascular flora and cryptogams, however, is not well understood. From studies in North America, [illegible] (1985) concluded that mosses in-[illegible] as forbs and grasses are progressively [illegible] by overgrazing. Studies in the semiarid woodlands of eastern Australia (Mucher et al. 1988) reported a strong positive relationship [illegible] vascular plant biomass and the [illegible] covered by cryptogamic [illegible]

The role of cryptogamic [illegible] is not well understood and [illegible] [illegible] been con[illegible] infiltration has been observed on areas with microphytic crusts compared to areas without (e.g., Blackburn 1975, Fletcher and Martin 1948, Gifford 1972, Yair 1990). However, other researchers (e.g., Brotherson and Rushforth 1983, Danin 1978, Graetz and Tongway 1986, Loope and Gifford 1972, Rogers 1977) showed that the presence of cryptogams of variable cover reduces infiltration.

As cryptogams are often associated with sparsely vegetated landscapes with high natural rates of erosion, it is natural to assume that they play a role in reducing erosion (West 1990). Claims of reduced water erosion due to cryptogamic crusts are widely reported in the literature (e.g., Campbell et al. 1989, Chartres and Mucher 1989, Greene et al. 1990, Kinnell et al. 1990, Mucher et al. 1988, Rushforth and Brotherson 1982, Yair 1990). The resistance of cryptogamic crusts to erosion is thought to be due to cyanobacteria and to a lesser extent fungi associated with the cryptogamic mats. Polysaccharides produced by cyanobacteria and fungal hyphae (Tisdall and Oades 1982) bind their cells, filaments, and surrounding soil particles into small aggregates (Shields and Durrell 1964). These aggregates have enhanced stability in water and help to protect the soil from wind

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and water erosion (Fletcher and Martin 1948, Greene and Tongway 1989).

The role of cryptogams in ecological processes in semiarid regions has received little attention until recent reviews by Harper and Marble (1988) and West (1990) appeared in the literature. These reviews draw heavily on published research from semiarid regions of North America, Australia, and Israel. In the semiarid rangelands of eastern Australia, research is currently underway to examine the spatial distribution of cryptogamic surfaces, their relationship to vascular plants and rangeland condition and trend, and their effects on infiltration and erosion.

In this paper I present preliminary results of research on the distribution of cryptogamic flora and their role in vascular plant dynamics, splash erosion, and infiltration.

MATERIALS AND METHODS

Study Area

All studies were undertaken at Yathong Nature Reserve and 'Coan Downs', approximately 140 km southwest of Cobar in western New South Wales, Australia (32°56′S, 145°35′E, Fig. 1). Sheep grazing on native pasture is the principal land use in the region. 'Coan Downs' is typical of grazing properties in the area where merino ewes and wethers are run in paddocks of approximately 2000–4000 ha. Yathong Nature Reserve has not been grazed by sheep, however, since 1977. It currently carries large populations of rabbits (*Oryctolagus cuniculus*), grey and red kangaroos (*Macropus giganteus*, *M. fuliginosus*, and *M. rufus*), and feral goats (*Capra hircus*; Leigh et al. 1989).

The climate of the area is characterized by a low and unreliable rainfall averaging 350 mm per annum. Rainfall is evenly distributed throughout the year, although winter rainfall (June–August) is slightly less variable than summer rainfall. Maximum and minimum diurnal temperatures range from 35.0°C and 19.6°C in January to 16.0°C and 3.6°C in July. The area receives on average 23 frost days per annum, and annual evaporation at Cobar to the north of the study area is approximately 2575 mm (Bureau of Meterorology 1961). The highest wind runs are experienced from spring and late summer (September–February), which correspond with the period of maximum soil erodibility.

Fig. 1. Location of the study area in eastern Australia.

Yathong Nature Reserve and 'Coan Downs' are located on the southern tip of the Cobar Pediplain on gently undulating plains to 3% slope derived from Paleozoic rocks including granites (Iwaszkiewicz and Semple 1988). The soils overlying much of this landscape are red and red-brown clay loams and loams (Typic Haplargids; Soil Survey Staff 1975), with gradational texture profiles containing variable amounts of stone and gravel.

Vegetation at Yathong Nature Reserve and 'Coan Downs' is open woodland dominated by red box (*Eucalyptus intertexta*), white cypress pine (*Callitris glaucophylla*), and wilga (*Geijera parviflora*). Understory pastures are dominated by speargrasses (*Stipa* spp.), wiregrasses (*Aristida* spp.), and various annual forbs.

Cryptogam Dynamics Study

In conjunction with the study of the role of cryptogams in infiltration (discussed below), data were collected on total cover of cryptogams and cover of various cryptogam types (i.e., mosses, algae, lichens, and liverworts). Data are presented for 43 locations from the ungrazed Yathong Nature Reserve and 34 locations from the grazed 'Coan Downs'.

Pasture Dynamics Study

As part of a larger study of the temporal changes in pasture dynamics (cover and species composition of vascular plants) and cover of cryptogams were recorded at regular intervals from nine large sites between September 1988 and February 1990. Each site measured 500 × 500 m. At each site, fifty 0.25 m^2 quadrats were periodically sampled and the following components measured: cover of perennial grasses, ephemerals, bare soil, litter and cryptogams, and total aboveground biomass of pasture. For the purpose of this study individual cryptogamic taxa have been pooled.

Infiltration Study

At Yathong Nature Reserve and 'Coan Downs' two sites were selected (independent of the nine pasture dynamics sites above) for investigating the role of cryptogam cover on two infiltration parameters: sorptivity (mm $h^{-0.5}$) and steady-state infiltration (mm h^{-1}).

Sorptivity is the initial rapid phase of infiltration, usually lasting less than 10 min, which is dominated by capillary forces. Steady-state infiltration, however, occurs during the latter stages of infiltration when only gravitational forces predominate. Steady-state infiltration is strongly related to soil porosity, which in turn depends on type and amount of cover.

At Yathong Nature Reserve, where soil surface and vegetation cover are in excellent condition, 44 locations were selected for infiltration measurements, i.e., 22 each for sorptivity and steady-state infiltration. At 'Coan Downs', unlike Yathong Nature Reserve, historical overgrazing has lead to the development of distinct zones of erosion and deposition known as production and sink zones, respectively. These commonly occur in landscapes where fluvial processes predominate. Together with an intermediate transfer zone, which has characteristics of both production and sink zones, these zones constitute what are known as erosion cells (Pickup 1985). At 'Coan Downs' 10 and 7 locations were selected for measurements of sorptivity in the production and sink zones, respectively, and 9 and 7 locations for measurement of steady-state infiltration in the two zones, respectively.

Locations for detailed measurements of sorptivity and steady-state infiltration were selected so that the soil surface under the base of the permeameter (diam = 21.2 cm) varied in cryptogam cover from 0 to 100%. Only areas in [illegible] evenly distributed under the [illegible] were selected. [illegible] is the boundary of complete [illegible] covered areas which [illegible] represented [illegible] infiltration [illegible] cover of cryptogams and relative contribution by various cryptogam types (i.e., lichens, mosses, algae, liverworts) were visually estimated, and color slides of each plot were taken to calibrate field estimates of total cover.

Sorptivity and steady-state infiltration were measured under ponded conditions, i.e., under a permanent pond of 10 mm of water. The ponded permeameter measures infiltration through all soil pores, i.e., matrix or small soil pores, and macropores (>0.75 mm in diameter), which are generally produced by roots and faunal activity. The ponded permeameter was placed on a steel ring that was gently tapped into the soil and sealed at the sides to prevent leakage. Infiltration runs were carried out until steady-state was achieved, usually within 30 min. Sorptivity and steady-state infiltration were calculated according to the method of White (1988).

Splash Erosion Study

Undisturbed cores of soil with associated cryptogams were collected from Yathong Nature Reserve by pushing 75-mm lengths of 90-mm-diameter PVC tubes into moist soil flush with the surface and excavating the intact tube. Cryptogam cover was estimated visually in the field by two observers prior to collection. One hundred thirty-five samples were collected representing five classes of cryptogam cover, i.e., completely bare (0%), 25%, 50%, 75%, and 100% cover. Cores were then transported to the laboratory, placed in a large tray beneath the simulator, and subjected to a simulated rainfall of 45 mm h^{-1} for 20 min. Each replicate consisted of nine cores in a three-by-three array under the simulator. Fifteen simulations (5 treatments × 3 replicates) were performed.

Runoff water and sediment were collected at the lower end of a collecting tray by using a vacuum pump at 2-min intervals. Sediment bulked across replicates was separated into five size classes: <0.0553 mm (silt and clay), 0.0553–0.0990 mm (very fine sand), 0.0991–0.2515 mm (fine sand), 0.2516–0.500 mm (medium sand), and >0.500 mm (coarse sand and a few aggregates) by gently washing through a nest of sieves.

Statistical Analyses

Simple regression and correlation analyses were used to examine the relationships between total cover and cover of various cryptogam types, cryptogam cover and vascular plant cover, and cryptogam cover and infiltration parameters.

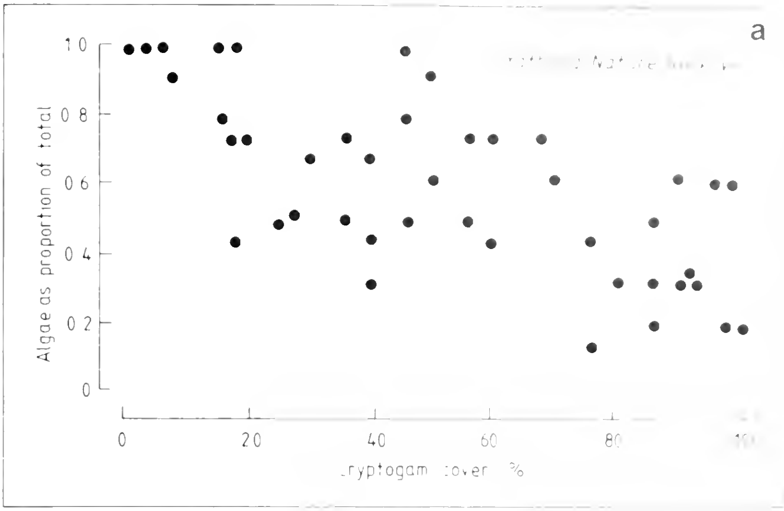

Fig. 2a. Relationship between cover of algae as a proportion of total cover and cryptogam cover at Yathong Nature Reserve.

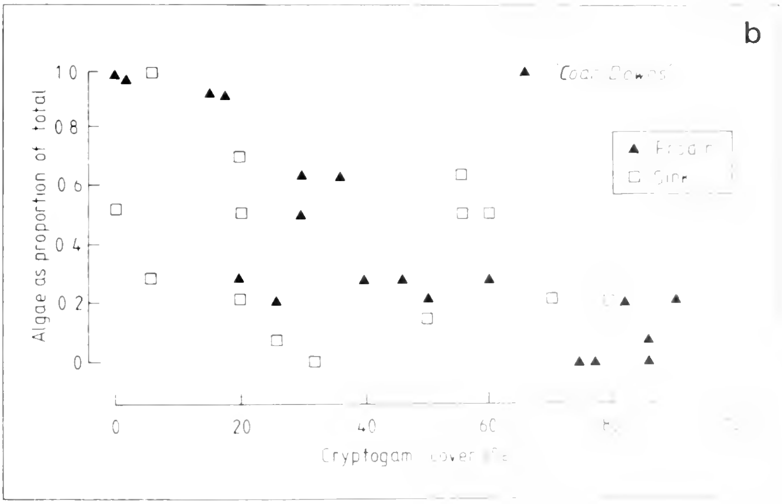

Fig. 2b. Relationship between cover of algae as a proportion of total cover and cryptogam cover at [illegible] 'Coach Downs.' Data are partitioned between the production and sink zones (see text for details).

Results are expressed as mean ± standard error of the mean (s.e.m.).

RESULTS

Cryptogam Dynamics

Sites with low total cover of cryptogams were dominated by algae, and, as cover increased, so did the relative contribution by mosses and some liverworts (Figs. 2a, 2b). Very few lichens were found at any location. When data were pooled across grazed and ungrazed sites, there was a significant negative correlation between total cryptogam cover and proportion of that cover comprising algae (R^2 = .28, P < .001, n = 77). Partitioning the data between grazed and ungrazed sites markedly increased the magnitude of the coefficients of determination for the ungrazed site (R^2 = .45, P < .001, n = [illegible]), but only slightly for the grazed site (R^2 = .31, P < .001, n = 34). Neither the slopes nor [illegible]

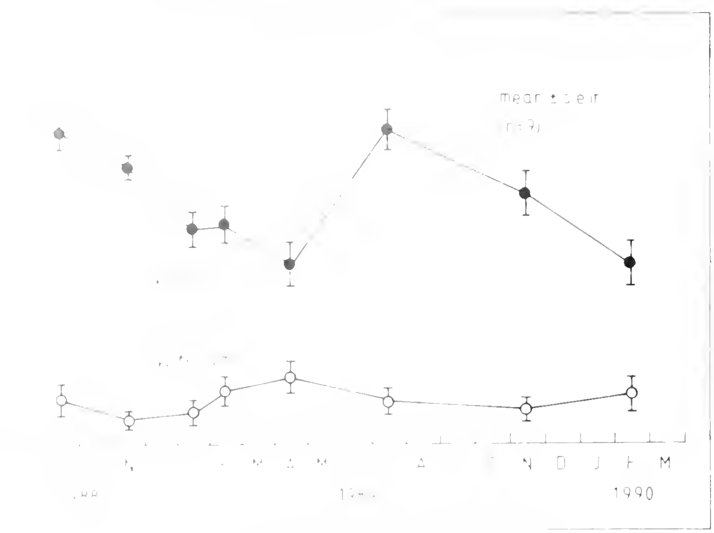

Fig. 3. Changes in cover (%) of cryptogams and vascular plants between September 1988 and February 1990.

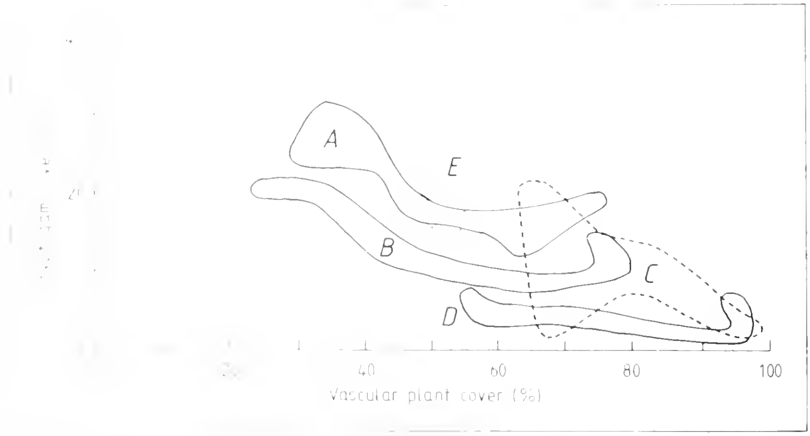

Fig. 4. Relationship between cryptogam cover (%) and vascular plant cover (%) for five groups of sites at Yathong Nature [illegible] Clusters depict changes between the eight sample dates shown in Figure 3. A = sites dominated [illegible] (sites 1 & 2), B = sites dominated by winter-growing ephemerals and *Aristida* spp. (3 & 4), [illegible] winter-growing ephemerals and *Stipa* spp. (7 & 8), D = gilgaid red earth sites dominated by [illegible] (sites 5 & 6), and E = site dominated by mixed summer- and winter-growing perennial grasses (9).

[illegible] relationships for the grazed or ungrazed sites were not significantly different.

Correlations Between Cryptogams and Vascular Plants

[illegible] cryptogam cover [illegible] from 2.5% to 17.6% [illegible] 45.7% to 96 [illegible] strongly negatively [illegible] biomass [illegible] biomass varied from 0.16 kg m^{-2} to 0.32 kg m^{-2}. Increasing biomass did not affect the magnitude nor the significance of the correlations between cryptogam cover and any of the independent variables. There was no evidence that high biomass levels were masking the presence of cryptogams on the soil surface. At all sites and times, cryptogam cover was negatively correlated with cover of litter, perennial grasses, and ephemerals and positively correlated with cover of bare soil.

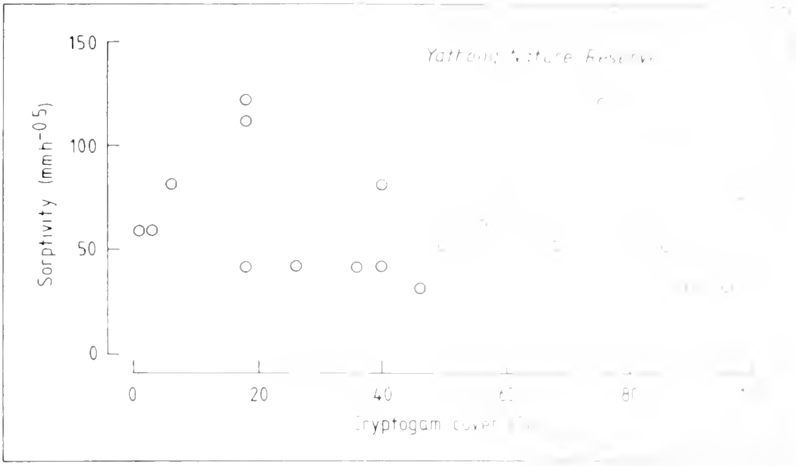

Fig. 5. Relationship between ponded sorptivity (mm $h^{-0.5}$) and cryptogam cover (%) at Yathong Nature Reserve.

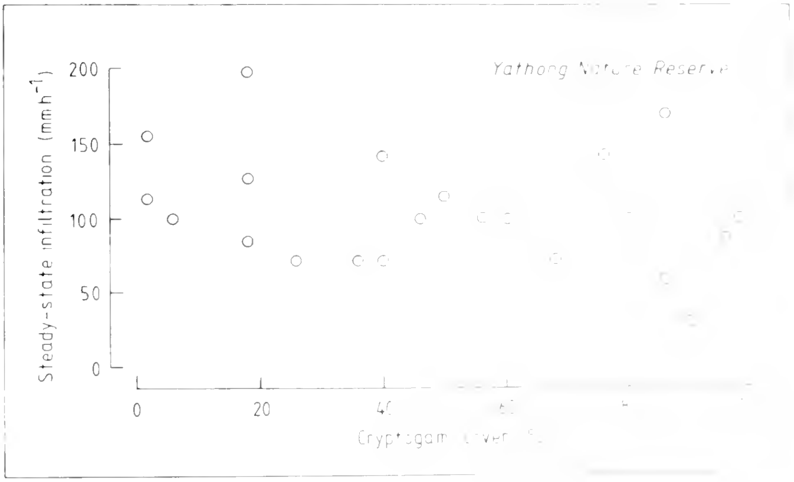

Fig. 6. Relationship between ponded steady-state infiltration (mm h^{-1}) and cryptogam cover (%) at Yathong Nature Reserve.

Temporal changes in cover of cryptogams and vascular plants varied between sites, with some sites fluctuating widely while others were more stable (Fig. 4). Perennial grass-dominant sites were generally the most stable. For example, there were only small changes in cryptogam cover on the gilgaid soils dominated by summer-growing perennial grasses (group D). Conversely, sites dominated by ephemerals (group A) experienced the largest fluctuations in cryptogam cover over time.

Infiltration

The relationship between cryptogam cover and the two infiltration parameters differed between grazed and ungrazed sites. At the ungrazed site at Yathong Nature Reserve, sorptivity averaged 62.9 ± 5.84 mm $h^{-0.5}$ (range 28–118 mm $h^{-0.5}$), and steady-state infiltration averaged 103.6 ± 8.3 mm h^{-1} (range 25–199 mm h^{-1}). Sorptivity was independent of cryptogam cover ($R^2 = .0$, $P = .473$, $n = 22$; Fig. 5), and there was a slight though insignificant decrease

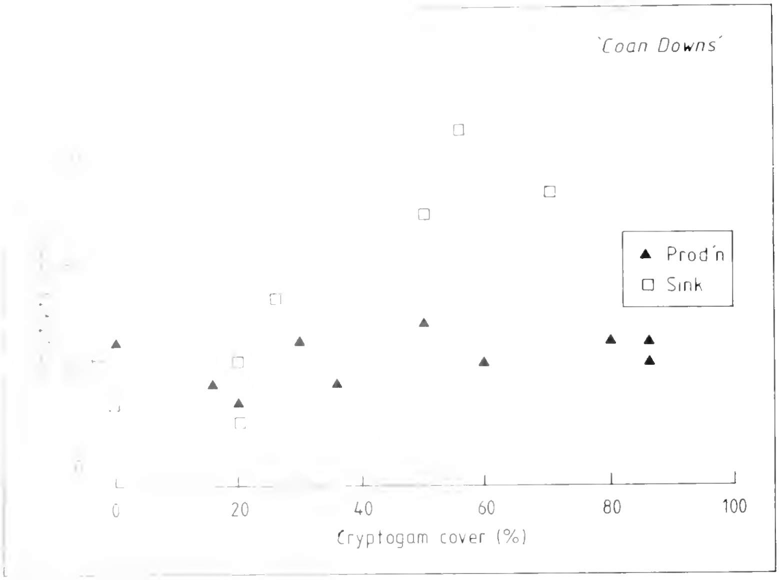

Fig. 7. Relationship between ponded sorptivity (mm h$^{0.5}$) and cryptogam cover (%) at 'Coan Downs'. Data are [illegible] between the production and sink zones.

in ponded steady-state infiltration with increasing cover (R [illegible] .0, P [illegible] .20, n = 22; Fig. 6).

At the grazed 'Coan Downs' site, sorptivity averaged 28.1 ± 3.7 mm h$^{0.5}$ (range 10–64 mm h$^{0.5}$) and steady-state infiltration averaged 39.7 ± 5.5 mm h^{-1} (range 11–103 mm h^{-1}). The high degree of variability within any one cover class meant that at low cover levels sorptivity and infiltration were sometimes low but sometimes high and vice versa. Consequently, the general trends of increasing sorptivity and steady-state infiltration with increasing cover were not significant (P = .121 and .053, respectively).

To account for a greater proportion of the variation in sorptivity and steady state infiltration, data were partitioned between the production and sink zones, the two major geomorphic [illegible] at the grazed site at 'Coan Downs'.

[illegible] positive relationship between [illegible] cryptogam cover at 'Coan [illegible] in the sink zone [illegible] but not in the [illegible] 10; Fig. [illegible] the same [illegible] positive [illegible] the sink [illegible]

Splash Erosion

Sediment removal increased significantly with decreases in cryptogam cover ($F_{1,10}$ = 45.8, P < .0001; Fig. 9). Little sediment was removed at cover levels >50%, but at lower levels than this, erosion increased markedly. The relationship between sediment removal and cryptogam cover was:

$$Y = e^{3.73-0.032c}$$

where Y is total sediment removal (g m^{-2}) and c is cryptogam cover (%). Cover of cryptogams explained 81% of the variation in sediment removal.

The rate of sediment removal varied among the five cover classes. Removal rates for the 100%, 75%, and 50% cover classes were very low and averaged 0.6, 2.0, and 3.2 g m^{-2} min^{-1}, respectively. The 25% and 0% cover classes, however, had a much higher rate of sediment removal (i.e., 8.8 and 15.3 g m^{-2} min^{-1}, respectively).

The particle-size distribution of eroded material was also influenced by cryptogam cover. As cover decreased, the proportion of silts, clays, and very fine sand increased and coarse sands decreased. Thus, not only was more sediment lost from soils with low cryptogam cover, but more of that sediment comprised silts and clays, onto which the majority of the nutrients are

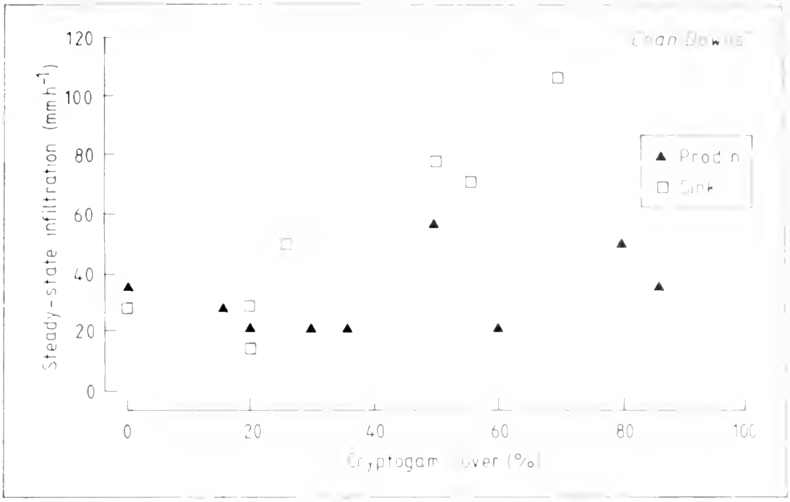

Fig. 8. Relationship between ponded steady-state infiltration (mm h^{-1}) and cryptogam cover (%) at Coan Downs. Data are partitioned between the production and sink zones.

bound. Furthermore, much of the fine material was removed during the early stages of runoff; i.e., as simulations proceeded, a higher proportion of coarse particles was removed.

DISCUSSION

In the semiarid woodlands of eastern Australia, overgrazing by domestic and feral animals over the past 100 years has resulted in a severe depletion of the native pastures (Harrington et al. 1984) and a shift from desirable perennial grasses to less desirable perennials and ephemerals (Iwaszkiewicz and Semple 1988). This has been accompanied by reduced productive potential of the soil and increased bare soil, runoff, and soil erosion (Johns 1983). In this environment vascular plant cover is highly discontinuous or patchy, and cryptogams are often the only biological soil cover providing protection from erosion.

Cryptogam Dynamics

In this study, plots with a low cover of cryptogams were dominated by algae, and plots with a high cover by mosses and some lichens. This is not surprising inasmuch as algae act as pioneers in plant succession (Isichei 1990), and as the soil surface becomes more stable, mosses and lichens gradually increase in dominance (Dunne 1989) at the expense of algae. Because of this successional sequence in development of cryptogamic crusts from algae-dominant to moss-dominant and lichen-dominant, the presence of a surface dominated by mosses and lichens might be used as an indication of the stability of the soil surface. There is some evidence (Eldridge unpublished data) that the more stable sites at Yathong Nature Reserve and Coan Downs, i.e., those dominated by perennial grasses, had higher covers of moss and some lichen compared with the less stable ephemeral sites.

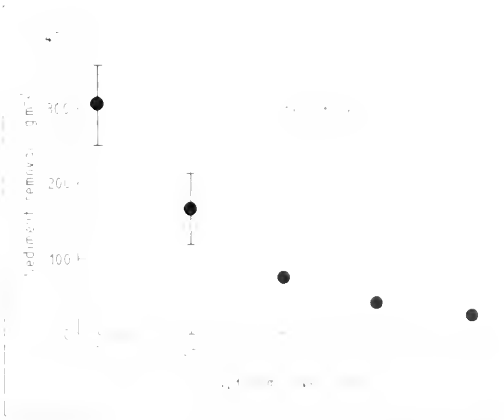

Fig. 9. Influence of cryptogam cover (%) on sediment removal (g m^{-2}) during 20 minutes of simulated rainfall. Symbols enclose standard errors of the mean except where shown (n = 3).

Cryptogams and Vascular Plants

In these studies decreases in vascular plant cover were associated with increases in the [illegible] (Fig. 1), [illegible] correlated with [illegible] cover of litter, perennial grasses, and [illegible], and positively correlated with cover of bare ground. This is consistent with studies from the semiarid shrublands of South Australia where cryptogam cover increased as cover of herbs and trees decreased following long-term exclusion of grazing (Crisp 1975). Similarly, Schofield (1985) reported that grazing increased the relative cover of mosses by reducing the cover of vascular plants.

The interaction between vascular plants and cryptogams has been described as a 1:1 tradeoff (West 1990), where a decrease in the proportion of one component results in an increase in the other. Thus, management practices leading to a change in the cover of vascular plants would ultimately affect the cover of cryptogams. Given an increase in vascular plant cover through exclosure or destocking, it is likely that cryptogam cover would decrease through increased competition for light and moisture and through overtopping by perennial grasses (Looman 1964).

In marked contrast to my results, numerous studies have reported positive correlations between cryptogam cover and vascular plant cover. For example, Graetz and Tongway (1986) showed a significant positive correlation between the cover of perennial chenopod shrubs and cover of cryptogams, and Mucher et al. (1988) described how biomass of biennial grasses and forbs increased as cover of cryptogams increased. In the desert grassland in Utah, Kleiner and Harper (1977) showed how [illegible] of vascular plants increases with [illegible] of nonvascular flora. Similarly, in the [illegible] desert of North America extensive [illegible] the vascular plant community [illegible] is associated with a [illegible] in the nonvascular flora ([illegible] communication). [illegible]

Infiltration

Although cryptogams have been reported as affecting infiltration, results from Yathong Nature Reserve and 'Coan Downs' indicate that other soil factors may be more influential. The positive linear relationship between cryptogam cover and infiltration on the grazed sites in this study is consistent with a few studies (Fletcher and Martin 1948, Gifford 1972) but is inconsistent with the bulk of published research suggesting that cryptogamic crusts reduce infiltration (see West 1990).

At Yathong Nature Reserve, where grazing by domestic animals ceased in 1977, there was a nonsignificant trend of decreasing infiltration with increasing cryptogam cover. The differences in response to changes in cryptogam cover may be explained in part by the differences in soil physical properties between the grazed and ungrazed soils. At a number of sites in Yathong Nature Reserve, Eldridge and Rothon (1992) found that changes in vascular plant cover explained very little of the variation in infiltration, runoff, and sediment yield. This is thought to be due to the high macroporosity status of the soil on the ungrazed sites, with infiltration determined by the overriding influence of soil physical properties.

On moderately degraded soil surfaces, a combination of a smooth soil surface with poorly developed microrelief and minimal obstruction from grass butts, stones, and litter creates a situation where there is little opportunity for runoff to enter the soil profile. This was certainly the case at 'Coan Downs' where soil physical properties were severely degraded, macroporosity was low, and the majority of infiltration was restricted to flow through the soil matrix and very small biopores. In this environment cryptogams probably have two principal effects. First, they provide a physical barrier on the soil surface, protecting the surface against raindrop impact and thereby ensuring that the existing low levels of structural stability are maintained. Second, as infiltration is predominantly through matrix pores, fungal hyphae in the cryptogams assist by maintaining the integrity of these pores so that small increases in cryptogam cover result in marked increases in infiltration (Figs. 6, 7).

Cryptogams are thought to impact upon the hydrological cycle by their direct effect on soil surface roughness. Cryptogamic crusts increase surface microrelief by cementing wind- and water-eroded fragments into cohesive units, producing a raised, roughened surface (Anderson et al. 1982). This increased surface roughness retards overland flow, allowing more time for infiltration and deposition to occur (Warren et al. 1986). However, direct measurement of the surface microrelief of some ungrazed soils at Yathong Nature Reserve showed that cryptogams are not consistently associated with rougher soil surfaces (Eldridge 1991).

Splash Erosion

The splash erosion studies reported here demonstrate that the presence of a cryptogamic crust significantly reduces splash erosion from a semiarid red earth soil. Soil surfaces with >75% cryptogam cover had very little erosion, while surfaces with 25% cover or less had erosion of at least an order of magnitude greater (Fig. 8).

Numerous studies (e.g., Chartres and Mucher 1989, Kinnell et al. 1990, Yair 1990) have shown the importance of cryptogam cover in reducing soil loss and erosion. Booth (1941) found that soil loss on soil with a cyanobacterial crust is 20 times less than that from the same soil with no crust. More recently Tchoupopnou (1989) showed that under simulated rainfall, cryptogam-covered surfaces reduce the distance over which splash soil particles are displaced.

Not only did surfaces with a low cover of cryptogams lose more soil during simulated rainfall, but more of that soil comprised silts and clays. Thus, the loss of fine material from the low cover plots probably represents a continual removal of nutrients from the low cover surfaces and, at least in the case of nitrogen, a possible decline in productivity. This compares with the high cryptogam cover soils where eroded material comprised mainly coarse-grained sands and some aggregates >0.500 mm in diameter. Mosses and algae bound some of the particles removed during the erosion process. Thus, erosion may be assisting the dispersal and deposition of these microphytic taxa within the landscape.

As this study used small cores taken from the field, it is not possible to assess the degree to which splashed sediment is redeposited within the landscape. The soil loss values reported here probably overestimate what happens in the field where litter and plant butts would trap some moving sediment.

CONCLUSIONS

This study showed that cryptogams play a major role in infiltration and erosion in the semiarid woodlands of eastern Australia. Furthermore, strong relationships exist within cryptogamic taxa, and between cryptogam cover and cover and biomass of vascular plants.

At Yathong Nature Reserve and 'Coan Downs', the presence of cryptogams on the soil surface had a variable influence on infiltrating water but significantly reduced the susceptibility of the soil to splash erosion. Infiltration at the grazed sites at 'Coan Downs' was markedly different from that at the ungrazed Yathong Nature Reserve, probably a result of differences in soil physical properties, particularly macroporosity.

Under simulated rainfall, surfaces supporting a high cover of cryptogams were more stable and less erodible than surfaces with low cryptogam cover. Erosion from cryptogamic surfaces of varying cover probably results in a transfer of fine material and nutrients from areas of low cover to areas of high cover. Ultimately, low cover areas become less accessible to establishment by seedlings of vascular plants. Furthermore, the role of cryptogams in soil stability is enhanced during drought periods when cover of the usual vascular plant is either absent or severely reduced.

ACKNOWLEDGMENTS

I thank John Pickard and Jeff Johansen for comments on earlier drafts of the manuscript and numerous colleagues for assistance with fieldwork. I am grateful to the Cullen-Ward family of 'Coan Downs' for allowing access to their property. The work was partially funded by the National Soil Conservation Programme of the Commonwealth Government of Australia under a permit from the NSW National Parks and Wildlife Service.

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CYANOBACTERIA AND CYANOLICHENS: CAN THEY ENHANCE AVAILABILITY OF ESSENTIAL MINERALS FOR HIGHER PLANTS?

Kimball T. Harper[1] and Rosemary L. Pendleton[2]

ABSTRACT—In both field and greenhouse studies, cyanobacteria and cyanolichens of cold-temperate deserts often enhance growth and essential element uptake by associated herbs. That effect is associated with better seedling establishment and larger seedlings. The following are possible mechanisms for these effects: (1) the microbiota concentrate essential elements in available forms in soil surface layers, (2) the microbial surface covers are usually darker colored than the soil itself and produce warmer soils during cool seasons when soil water is most available, (3) the gelatinous sheaths of several cyanobacterial genera common on alkaline deserts contain chelating compounds, and (4) conditions that favor persistent microbial growths on soil surfaces also favor maintenance of larger populations of microorganisms that form mycorrhizal and/or rhizosheath associations with seed plants. There is evidence that associated animals may be nutritionally benefited by the enhanced mineral content of forage plants growing in well-developed cyanobacterial crusts.

Key words: cryptogamic crusts, mineral uptake, plant nutrition, plant growth, mycorrhizae, deserts, cyanobacteria, Collema, Microcoleus.

Dense growths of cyanobacteria, lichens, xerophytic algae, mosses, and microfungi are a common feature of soil surfaces in semiarid and arid temperate regions worldwide (Friedmann and Galun 1974, Harper and Marble 1988, West 1990). Such soil covers are commonly much darker than associated surfaces without such growths (Fig. 1). Previous work on these cryptobiotic surface growths (or "cryptogamic crusts" as they are often called) has focused on their ability to "fix" nitrogen in a biologically available form (MacGregor and Johnson 1971, Mayland et al. 1966, Shields and Durrell 1964) and to stabilize soil surfaces against water (Booth 1941, Fletcher and Martin 1948, Fritsch 1922) or wind erosion (MacKenzie and Pearson 1979). Other studies have shown that nitrogen fixed by cyanobacterial components of the cryptobiotic crusts is available to higher plants (Fuller et al. 1960, Mayland and MacIntosh 1966, Stewart 1967).

The intent of this paper is to assemble existing data and report new data bearing on the influence of cyanobacterial-rich assemblages of cryptobiota on mineral nutrition of associated vascular plants.

PERTINENT LITERATURE

A large literature documents the role of cyanobacteria, cyanolichens, and free-living bacteria (nonsymbiotic) in desert soils (Harper and Marble 1988, West 1990). Since legumes and other vascular plants that form symbiotic, nitrogen-fixing associations with bacteria are uncommon in cold-temperate deserts, their importance as sources of biologically available nitrogen is minimal in such environments (West 1981). Rychert et al. (1978) concluded that "blue-green algae"–lichen crusts fix significant amounts of atmospheric nitrogen in desert soils (they estimate fixation of 10–100 kg N $ha^{-1} yr^{-1}$ in the Great Basin of North America). Available information suggests that nonsymbiotic, heterotrophic nitrogen fixers are responsible for fixation of only ≤2 kg N $ha^{-1} yr^{-1}$ in North American deserts (Rychert et al. 1978, Steyn and Delwiche 1970). The input of available nitrogen in annual precipitation is apparently low, with estimates running from 4–6 kg $ha^{-1} yr^{-1}$ (West 1978) to 1–2 kg $ha^{-1} yr^{-1}$ (Schlesinger 1991). Schlesinger (1991) notes that available N in dry-fall exceeds that in rainfall in some areas, but West and Skujins (1978) argue that since deserts produce

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FIG. 1. Contrast between natural soil color and the dark-colored cryptobiotic growth on the soil surface. Such surface growths of cyanobacteria, the black lichen *Collema*, and xerophytic mosses are common on desert soils in the Intermountain West of North America. Soil shown is developed from ancient lacustrine deposits, western Utah.

more dust than they receive. N in dust (the primary source of N in dry-fall) probably represents a net export from deserts. Denitrification processes are active in deserts and may equal or exceed rates of fixation (Skujins and Klubek 1978).

It is estimated that vascular plants take up [illegible] kg N/ha/yr in the cold deserts of the Great Basin (West and Skujins 1977). We can deduce from data by Romney et al. (1978) that [illegible] of N by vascular plants in the [illegible] northern Mohave is slightly [illegible] by West and Skujins [illegible]. In either case, annual [illegible] of new [illegible] heterotro[illegible] N fixed by [illegible]

surface soils of deserts has been documented in a variety of reports. Such studies often show that available P, exchangeable K, and surface soil organic matter increase apace with cryptobiotic cover (Anderson et al. 1982, Kleiner and Harper 1972, 1977a, 1977b, McKnight 1980). The trend for elements other than N is apparently related, at least in part, to the tendency of the cryptobiotic crusts to trap soil fines (silt and clay) and to sequester essential elements in living cells (Fletcher and Martin 1948, Kleiner and Harper 1972).

Cryptobiotic crusts are usually darker than associated soils in deserts (Fig. 1). As a result, soil surfaces covered by such crusts absorb radiant energy better than nearby uncrusted soils and are warmer (Kleiner and Harper 1977b, Harper and Marble 1988). Temperature differences may be at least 5°C (Harper and Marble 1988) and are probably greatest in cooler seasons. In the Great Basin, where the bulk of biologically usable moisture accumulates from winter storms, areas covered by cyanobacterial-*Collema* lichen crusts can be expected to be significantly warmer than interspersed uncrusted soils. Both soil microbes and associated vascular plants (especially shallowly rooted species and seedlings) should experience accelerated spring growth on sites where soil temperature is elevated because of well-developed cryptobiotic growth. Enhanced growth of seed plants rooted in cryptobiotic crusts might be expected because of more favorable temperatures and more fertile soils. Physiologists have long recognized that many physiological processes have a Q_{10} of 2–3; that is, as temperatures within the range of easy tolerance are increased 10°C, metabolic rates for processes such as enzymatic reactions, ion uptake, and ion transport are doubled or tripled (Glass 1989).

Algologists and microbiologists have documented the nature of organic secretions from microorganisms and speculated on their ecological roles in the organism-environmental complex. Algae are known to secrete polysaccharides, amino acids, vitamins, growth factors, steroids, saturated and unsaturated fats, and other beneficial or toxic compounds of unknown structure (Lefevre 1964). The secretions often form a gelatinous film around the cells. Among cyanobacteria, such sheaths are common and include polysaccharides, organic acids, amino acids, and polypeptides (Lange 1974). In aquatic systems, extracellular organic secretions play a variety of roles including food for heterotrophic organisms, chelating agents that increase availability of essential elements (particularly iron and other trace elements), growth stimulators, toxic compounds that discourage herbivory (and are sometimes autotoxic), and compounds that complex with and inactivate toxic agents (such as copper) in water (Lefevre 1964).

Lange (1974) demonstrated that sheath materials of cyanobacteria include chelating agents that permit the organisms to grow vigorously in water having a high pH in which several essential elements would otherwise be available in such low amounts that active growth would be impossible. He demonstrated that some species in each of the following genera secreted enough natural chelators to produce growth equivalent to that of the same species in cultures that received artificial chelators: *Anabaena*, *Anacystis*, *Lyngbya*, *Microcystis*, and *Nostoc*. He also demonstrated that the natural chelators were water soluble and that filtrates of cultures in which chelating species had grown supported good growth of nonchelating species. The latter species were unable to grow in the same water if chelating species had not previously grown in it. Lange (1976) concluded that the gelatinous sheaths of cyanobacteria provide a microenvironment around their cells, where essential nutrients can be concentrated from an environment in which those elements exist at levels too low to sustain growth. In alkaline deserts the hygroscopic nature of the copious gelatinous sheaths produced by cyanobacteria (and many associated algae, bacteria, and fungi) suggest another, perhaps essential, role for such extracellular secretions, that of retaining enough water around cells in dry periods to prevent lethal desiccation.

A large literature documents the important role of mycorrhizal associations for mineral nutritional relationships of vascular plants (Allen 1991). Allen (1991) concluded that "major perturbations almost always reduce the inoculum density" of mycorrhizal fungi. Bethlenfalvay et al. (1985) determined that trampling of soils by hoofed grazers (cattle) reduced mycorrhizal inoculum in crested wheatgrass pastures in Nevada. Koide and Mooney (1987) showed that pocket gopher burrowing in otherwise undisturbed serpentine herblands in coastal California also reduced mycorrhizal inoculum. Perry et al. (1989) reported that sprouting shrubs may maintain a mycorrhizal infection through the stressful conditions induced by wildfire. Wullstein and Pratt (1981) discussed the development of rhizosheaths of *Oryzopsis hymenoides* (R. & S.) Riker (now classified as *Stipa hymenoides* R. & S.), a desert grass. *Oryzopsis* and several other grasses of arid, sandy soils produce conspicuous rhizosheaths consisting of dense tangles of root hairs and intermixed heterotrophic bacteria capable of fixing nitrogen (Wullstein et al. 1979). Unpublished data in the files of the senior author suggest that rhizosheaths apparently enhance mineral uptake of *Stipa hymenoides* for several elements.

The foregoing literature survey suggests that cryptobiotic crusts may significantly alter the uptake of essential elements by associated desert seed plants. In this paper we report preliminary results on the effects of cryptobiotic covers dominated by cyanobacteria and *Collema* on tissue chemistry of associated seed plants. *Collema* is a black-colored lichen in which the photobiont is the cyanobacterium *Nostoc*. Specifically, we will consider the effects of the [illegible] 7 cm [illegible] of [illegible] composite samples [illegible] at three [illegible] Wind Whistle [illegible] County, and 12 composite samples [illegible] soils stabilized by [illegible] at Arches National Park [illegible]

[illegible]	Blow sand	Cyanobacterial *Collema* sand
Sand	92.7	79.1
Reaction pH	7.8	7.2
	Percent	
Organic matter	0.057	0.93
Nitrogen	0.008	0.021
	PPM available	
Calcium	[illegible]449	3,784
Copper	0.20	0.21
Iron	8.4	7.5
Magnesium	39.0	57.0
Manganese	4.6	15.4
Phosphorus	23.7	51.8
Potassium	69.7	87.0
Sodium	8	10
Zinc	0.5	0.3

cryptobiotic cover on soil fertility, soil temperature in the cool season, possible chelation effects, and colonization of seed plant roots by microorganisms.

METHODS

[illegible] considered in Tables 1 and 3 [illegible] composite samples of the surface 5 [illegible] at 10–12 randomly cho[illegible] each of the following surface [illegible] supported a well devel[illegible] bacteria and [illegible] areas only [illegible] winds or [illegible] development [illegible] in [illegible] the [illegible]

paste. Organic matter was estimated by digestion with 1.0 N potassium dichromate. Total soil nitrogen was analyzed by the micro-Kjeldahl procedure. Phosphorus was determined with the iron-TCA-molybdate method on a soil extract taken with 0.2 N acetic acid. Exchangeable bases were freed from the soil with 1.0 N ammonium chloride. Ion concentrations in the extract were estimated by atomic absorption. All soil analyses were made in the Soil and Plant Analysis Laboratory, Department of Agronomy and Horticulture, Brigham Young University, and all analytical methods were based on those recommended by Black et al. (1965).

Soils for pot trials in the glasshouse were bulk-collected from the Sand Flats site, Grand County, Utah, in January 1991 and immediately spread in a thin layer on a laboratory floor to air-dry. Samples from areas with and without cryptobiotic cover consisted of the surface 5 cm only. Once dried, soils from each surface type were thoroughly mixed (including the biotic cover for that sample set) to ensure a uniform potting mixture. No fertilizer amendments were added. Subsamples from each surface type were taken for subsequent analysis of physical and chemical characteristics. One liter of soil from the sample taken from each surface type was placed in a drained plastic pot having a top diameter of 15 cm. Before pots were filled, drainage holes were covered with a coarse fiberglass mesh to preclude loss of soil. Soils from each surface type were replicated 10 times in individual pots. Pots were immediately placed in a grid on a water-tight table in a glasshouse and watered from the bottom with a 2.5-cm layer of water that was drained off as soon as soil at the pot surface was thoroughly wetted by capillarity. Pots were placed in a 4 × 5 grid with grid intersections 30 cm apart. Cryptobiotic and blow sand soil surface types were alternated in the grid. Six presoaked seeds of *Sorghum halepense* (L.) Pers. were planted in each pot on 11 February 1991. Pots were irrigated with tap water as needed to maintain nonstressful growing conditions.

To evaluate the effects of cyanobacterial growth throughout the rooting zone, we initiated a second trial simultaneously with the foregoing pot trials. In that trial we filled narrow, glass-walled planters with 0.9 liter of the same cryptobiotic-covered soil. Each planter was 1.5 cm wide, 40 cm long, and 30.5 cm deep and was divided into two compartments of equal size by a redwood strip 1.5 × 0.5 × 30.5 cm inserted at the midpoint of the planter before adding soil. The glass walls of one compartment of each planter were covered with aluminum foil to exclude light. Planters were drained and aerated at their bottoms via a perforated tygon tube (4 mm in diameter) open to outside air at both ends. These planters were irrigated and planted with presoaked *Sorghum halepense* seed at a rate of 6 seeds per compartment on 16 February 1991. This trial was replicated 10 times. It was necessary to water these planters on alternate days with 250–300 ml of water. For convenience, tap water was drawn and stored in a plastic bucket in the glasshouse until needed for irrigation of planters. This water averaged 8–12°C warmer than water taken directly from the tap. The combination of warmer irrigation water and less exposed soil surface from which water could evaporate resulted in root temperatures for plants grown in narrow planters that averaged 3–8.5°C warmer than those of *Sorghum* plants from the same seed lot grown in the same soil but watered from the bottom. Temperature differences were greatest immediately after irrigation of the pots with cold tap water.

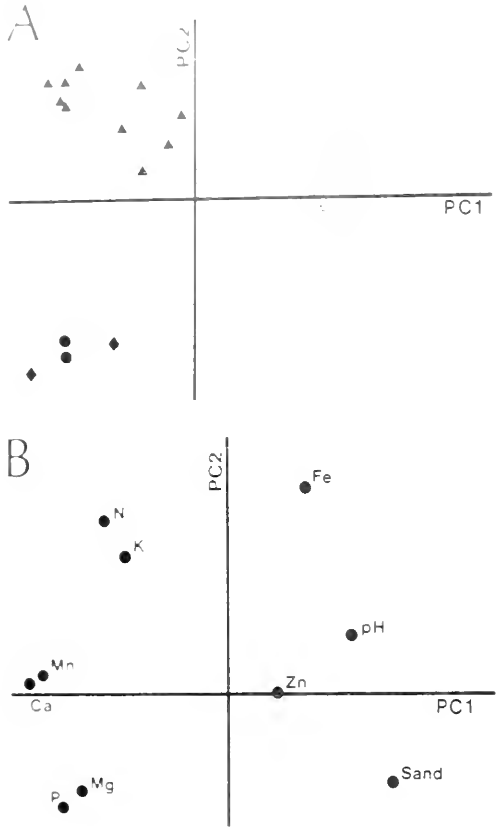
After three weeks cyanobacterial growth covered the glass walls of planters not covered by aluminum foil. The cyanobacteria obviously competed with *Sorghum* roots for essential minerals. Plants grown in planters that received light throughout the rooting zone were smaller, and their leaves were discolored by reddish pigments in contrast to adjacent plants grown under identical conditions except that light was excluded from the rooting zone. As a consequence, glass walls of all planter compartments were covered with aluminum foil 3 weeks after planting. The foil remained in place until plant top growth was harvested for analysis on 29 April 1991. Plants grown in planter compartments previously illuminated in the rooting zone quickly regained normal leaf color and became indistinguishable in size from adjacent plants grown in compartments with foil-covered rooting zones. Chemical analyses of plant tissue from these trials demonstrated that tissue chemistry from plants that had their rooting zone exposed to light for 3 weeks did not differ significantly for any element considered from that of plants that had not received light at any time in the rooting zone.

Plants in narrow planters and those in pots of bottom-irrigated, cyanobacterial-enriched soil were grown from the same seed lot in the same soil and were propagated in the same glasshouse at the same time. These otherwise identical conditions for growth were marked by a strong difference in root temperature, with pots averaging ~16°C and narrow planters ~21°C. To determine the effect of different rooting zone temperatures on mineral composition of *Sorghum* aboveground growth, we analyzed and compared the chemical composition of top growth of pot-grown plants and planter-grown plants (see Results).

Plant tissue was oven-dried at 60°C for 12 hr and then ground in a steel rotary mill using a 40-mesh sieve. Samples were stored until analyzed in capped plastic vials. Tissue nitrogen was determined using micro-Kjeldahl procedures. Duplicate 1.0-g tissue samples from each experimental replication were digested in a 1:5 solution of concentrated sulfuric and nitric acid. Content of bioessential elements in the digestate was determined using atomic absorption procedures (Page et al. 1982).

The degree of root infection by vesicular arbuscular mycorrhizae and other root symbionts such as *Rhizobium* bacteria (associated with roots of *Lupinus*) or *Bacillus* bacteria (associated with rhizosheaths of *Stipa hymenoides*) was determined by microscopic examination of roots of randomly selected plants growing in well-developed cyanobacterial-*Collema* crust or on nearby comparable sites where wind action or animal traffic (sometimes areas trampled by people) had precluded growth of cryptobiota. Within each soil surface type, plants were randomly selected using the quarter method (Cottam and Curtis 1956). Plants were collected during early flowering (early May 1992) in Washington and Grand counties, Utah. *Bromus tectorum* L., *Cryptantha pterocarya* (Torr.) Greene, *Cryptantha crassisepala* (T. & G.) Greene, *Festuca octoflora* Walter, *Lupinus pusillus* Pursh, and *Plantago patagonica* Jacq. were collected in Washington County. *Coleogyne ramosissima* Torr., *Mentzelia albicaulis* Doug. ex Hook., *Stipa hymenoides*, and *Streptanthella longirostris* (Wats.) Rydb. were collected in Grand County.

Using a shovel, we lifted the root systems from the sandy soils in a block and then freed them from associated sand by hand. Plant tops were immediately excised and roots were placed in 75% ethanol in labeled, screw-cap glass



[illegible]

Plant nomenclature follows Welsh et al. (1987). Lichen nomenclature follows Egan (1987). Statistical significance of differences between group means was determined using an unpaired t-test model (Snedecor and Cochran 1967). Significance of treatment effects in Table 5 was determined using analysis of variance (ANOVA) with species treated as blocks. Percentage data were arcsine transformed prior to analysis by the GLM procedure of the SAS statistical package.

Centered, standardized principal components analysis (PCA) was used to analyze differences among samples collected from crusted soils and uncrusted soils (Pielou 1984). Various soil chemical and physical parameters were used in this analysis, which was conducted using the Statgraphics package.

RESULTS

The effect of cryptobiotic growth on surface soil chemistry and texture is particularly impressive for such variables as organic matter, soil N, exchangeable Mn, and "available" P (Table 1). Exchangeable Ca was also much higher on average in soils stabilized by cyanobacterial-rich surface growth. As in other studies (Fletcher and Martin 1948, Kleiner and Harper 1972, 1977a, 1977b), our results show that soil silt and clay are much greater in soils stabilized by cryptobiotic growth. The response of Ca, Mn, and P may be related to textural differences alone (Black 1968), but the increase in soil organic matter and N is probably directly related to the presence of cryptobiota.

Principal components analysis of the basic data on which Table 1 is based showed marked differences between crusted and uncrusted soils even though three separate areas (two in Arches National Park and one at Wind Whistle Campground) were studied. The first principal component clearly separated the crusted soils of the most intensively sampled Arches site from corresponding uncrusted soils samples (Fig. 2B). Crusted and uncrusted soils of the other [illegible] were also separated by the first component [illegible] differences among sites were evident [illegible] separation that occurred on the [illegible]pal component (Fig. 2A). The per[illegible]ariance in the data accounted for [illegible] PC2 were 48% and 22%, respec-

TABLE 2. Tissue elemental content of plants of *Festuca octoflora* (a diminutive annual) and *Mentzelia multiflora* (a short-lived perennial herb) grown on blow sand and nearby sand stabilized by cyanobacterial-*Collema* crusts. The *Festuca* samples were taken at Wind Whistle Campground in San Juan County, Utah; the *Mentzelia* samples were taken at Courthouse Wash Dunes, Grand County, Utah. All data are from Belnap and Harper (in review). All tissue concentrations are expressed as amount per unit dry weight of aboveground growth and attached root tissue brushed free of sand. Sample size was 5 for each mean.

	Festuca octoflora			*Mentzelia multiflora*		
	Soil surface condition			Soil surface condition		
Element	Cyanobacteria lichen cover	Blow sand	Sign. differ.	Cyanobacterial lichen cover	Blow sand	Sign. differ.
N (%)	2.25	1.95	*	2.61	2.18	**
P (%)	0.25	0.14	***	0.20	0.24	**
K (%)	1.88	1.64	*	3.04	2.67	NS
Ca (%)	0.65	0.52	***	2.50	1.97	NS
Mg (%)	0.15	0.13	**	0.33	0.23	*
Cu (ppm)	11.0	10.4	NS	8.6	9.0	NS
Fe (ppm)	300.3	149.4	*	639.8	465.4	*
Mn (ppm)	60.3	74.0	NS	98.2	82.4	NS
Na (ppm)	61.5	59.8	NS	77.2	63.4	*
Zn (ppm)	43.0	33.0	NS	22.0	20.0	NS

*Means significantly different at $p < .05$
**Means significantly different at $p < .01$
***Means significantly different at $p < .001$
NS Means not significantly different

Plotting the component weights (Fig. 2B) yields an explanation for the separation of crusted and uncrusted soils. The first component most clearly represents the differences between uncrusted and crusted soils. Uncrusted soils have higher values on this axis, which means they have higher pH and sand content (positive weights) and lower Ca, Mn, P, Mg, N, and K (negative weights). Iron and Zn tended to be higher in uncrusted soils but were not as important in separating points on the first axis. The second component most clearly represents site-specific differences. One Arches site (triangles in Fig. 2A) had higher N, K, and Fe (positively weighted) and lower P, Mg, and sand (negatively weighted) than the other two sites (Fig. 2B). The principal components analysis shows that despite some site-specific differences, crusted soils are generally higher in some essential minerals (N, K, P, Ca, Mg, Mn) than are uncrusted soils. Site differences were also clearly delineated in the analyses.

Table 2 clearly shows that cryptobiotic crusts do have a significant influence on tissue content of several bioessential elements in both *Festuca octoflora* and *Mentzelia multiflora* (Nutt.) Gray. Since Belnap and Harper (in review) show that soil textural differences are small (<10% difference in percentage sand) between blow sand and adjacent sands stabilized by surface growth of cryptobiota, the tissue content differences seen in Table 2 would seem to be strongly influenced by microorganisms on the soil surface. Tissue content of both seed plants was significantly greater for N, Mg, and Fe when plants were rooted in cyanobacterial-rich crusts. Although not all differences were statistically significant, 9 of 10 elements were present in greater amounts in tissue of *Festuca* plants grown on cryptobiotically stabilized surfaces; 8 of 10 elements were present in greater amounts in tissue of *Mentzelia* plants grown on the cryptobiotic surfaces. Finally, the data suggest possible competition between cryptobiota and seed plants for P and Mn. We also note that the responses of *Festuca* and *Mentzelia* were unalike in respect to P and Mn uptake.

Glasshouse trials demonstrate the soil "fertilization" effect of the cyanobacterial-*Collema* cover for growth of *Sorghum* (Tables 3, 4). Differences observed between chemistry of cyanobacteria-free and cyanobacterial-*Collema*–covered soils (Table 3) are small. The cryptobiotic-covered soil had slightly more N, P, K, and Na. The soil free of cryptobiotic growth averaged somewhat higher in Ca and Fe than the samples supporting cryptobiotic growth.

[illegible] (Table 3) [illegible] by [illegible] Sand [illegible] ments [illegible] which [illegible] (Table 4) [illegible] grown

[illegible]

[illegible]	Lacking cryptobiotic growth	Heavy cyanobacterial-*Collema* cover
[illegible]	58	61
[illegible] (pH)	7.5	7.4
[illegible]	1.00	0.95
N [illegible]	0.038	0.047
Ca [illegible]	2,670	1,845
Cu [illegible]	0.4	0.2
Fe [illegible]	5	2
Mg [illegible]	78	78
Mn [illegible]	5.1	3.1
P [illegible] available	58	47
K [illegible]	85	93
Na [illegible]	7	10
[illegible]	8	9
[illegible]	2	4

Given the small physical and chemical differences between soils (Table 3), the often significant differences in *Sorghum* tissue chemistry when grown on those soils (Table 4) were unexpected. Nitrogen and Zn were taken up in significantly greater amounts on the cyanobacterial-*Collema* enriched soil, producing [illegible] 5 times more top growth than soils with no cryptobiotic growth (Fig. 3). The elements Cu, P, Mn, and Na were present in significantly [illegible] concentrations in tissue of plants grown on the cryptobiotic-free soil. These data suggest [illegible] N or Zn (probably the former) is limiting [illegible] the test soil and (2) there is [illegible] between the cyanobacte- [illegible] P, Mn, and Na.

[illegible] nutrient uptake by [illegible] soil temperature [illegible] Ca, Mg, Cu, [illegible] apparently larger [illegible] soil [illegible]

crust-free soils on infection of roots by rhizosymbionts show that 6 of 10 species evidenced infection by root symbionts (Table 5). Of those species whose roots showed some infection, 4 of 6 were annuals, and all infected annuals were colonized by vesicular arbuscular mycorrhizae (VAM). The degree of infection was always greater for plants grown in cyanobacterial-*Collema* crusted soil. Seedlings of the shrub *Coleogyne ramosissima* supported heavier VAM infection than associated annuals, and the relative amount of root colonized by the root symbiont was over three times greater when seedlings emerged from crusted soils. Roots of the perennial grass *Stipa hymenoides* always developed rhizosheaths on both types of surface, but the degree of sheath development was greatest on crusted surfaces (Table 5). The overall effect of crusted soils on root infection by symbionts was positive and statistically significant (Table 5).

Discussion

The results presented provide strong support for the hypothesis that cryptobiotic soil surface covers (at least those rich in cyanobacteria) have significant effects on uptake of bioessential elements by associated seed plants. In this study we have considered only species (or developmental stages) with a major portion of their root system distributed in the surface 5 cm of soil. The cryptobiotic surfaces appear to consistently enhance uptake of some elements (e.g., N, K, Ca, Mg, and Zn), and to at least occasionally reduce uptake of other essential elements such as P, Fe, Mn, and Na (Tables 2, 4). Those effects are apparently partially explained by enrichment of soils (increased "availability" of essential elements) by cyanobacterial-*Collema* crusts (Table 1, 3), by elevation of soil temperature during cool seasons when moisture is most likely to be readily available for plant growth, and by greater likelihood of root colonization by mycorrhizal fungi and other root symbionts at sites that are stable enough to support well-developed cryptobiotic crusts. Our preliminary results also suggest that cyanobacterial-*Collema* crusts may result in an enhanced availability of certain elements through accelerated decomposition or production of chelating compounds (e.g., Mn and P in Table 1; Cu, N, Mg, and Zn in Table 4). Taken together, the data in Tables 3 and 4 suggest that the enhanced uptake of N by

TABLE 4. Tissue chemistry of aboveground growth of *Sorghum halepense* grown in cyanobacterial-*Collema*-free sand or sand heavily covered (over 80%) by cyanobacteria and *Collema* in pots wetted from the bottom. Also shown is tissue chemistry of *Sorghum* grown in the same cyanobacterial-*Collema*–stabilized sand held in deep, narrow rectangular planters. Averages followed by the same lowercase letter do not differ significantly ($p < .05$).

	Soil and potting conditions		
Tissue content of	Cyanobacterial-free soil in pots	Cyanobacterial soil in pots	Cyanobacterial soil in narrow planters
		Concentration (% dry wt.)	
N	0.67 a	0.78 b	1.41 c
P	0.15 a	0.12 b	0.09 c
K	2.29 a	2.41 a	2.27 a
Ca	0.57 a	0.44 b	0.64 a
Mg	0.15 a	0.14 a	0.26 b
		Concentration (ppm dry wt.)	
Cu	4.8 a	5.5 a	8.8 b
Fe	86.3 a	51.8 a	27.6 b
Mn	64.4 a	53.0 b	47.1 c
Na	114.3 a	32.6 b	50.7 c
Zn	15.7 a	22.6 b	23.9 b
Sorghum yield/pot (g-top growth only)	1.3 a	4.8 b	—
No. of replications	10	10	10
Avg. rooting zone temp (C)	~16	~16	~21

plants grown on crusted soils must include a considerable amount of N fixed simultaneously by cyanobacteria in the culture or N released by microorganisms decomposing the tissue of cyanobacteria grown during the experiment. Original differences in soil N were too small to account for the large differences observed in plant uptake in the two cultures.

Other studies have shown results similar to those reported here. Marble (1990) demonstrated that scalping the surface 1.0 cm of cyanobacterial-*Collema* crust around rosettes of *Lepidium montanum* var. *montanum* Nutt. two months prior to flowering significantly reduced aboveground plant weight and tissue content of K, Na, and Cu at flowering time. Several other elements (Ca, Mg, Fe, Mn, and Zn) were also lower in tissue of plants around which the cryptobiotic crust had been removed, but those differences were not statistically significant ($p >$ .05). J. Belnap (unpublished) has analyzed plant tissue for the annual *Streptanthella longirostris* (Brassicaceae) and seedlings of *Coleogyne ramosissima* (Rosaceae) grown on well-developed cyanobacterial-*Collema* crusts and on comparable soils without such crusts. Her data show that average plant size of both species was significantly larger on crusted soils, and tissue of both species contained significantly more N, Ca, Mg, and Cu per unit dry weight when grown on cryptobiotic surfaces. Belnap also has unpublished leaf chemistry data for adult shrubs of *Coleogyne ramosissima* and the long-lived, woody-rooted herb *Lepidium montanum* var. *jonesii* (Rydb.) C. L. Hitchc. As one might have predicted, adult plants of these species showed no enhancement of essential mineral uptake while growing on cyanobacterial-rich crusts. The vast majority of their feeder roots lie well below those portions of the soil profile that are influenced by cryptobiotic crusts.

As seen in Table 4, *Sorghum* growth was severely limited on soils free of cyanobacterial-*Collema* inoculum (Fig. 3). Nitrogen seemed inadequate in such soils to support healthy growth of *Sorghum*. In fact, growth was so minimal

Fig. [illegible]. *Sorghum halepense* plants after 60 days of growth on a soil mixture consisting of the surface 5 cm of a sand [illegible] (R) [illegible] growth of cyanobacteria and *Collema tenax* (R) and the same depth horizon from a nearby site kept [illegible] by foot traffic (L). See Table 3 for characteristics of the two soils.

[illegible] those soils that the species would probably never have flowered and set seed on that substrate. When *Sorghum* was grown on a soil enriched by inclusion of the cyanobacterial-[illegible] inoculum, growth was much greater [illegible] only N and Zn occurred in significantly greater concentrations in the tissue, i.e., [illegible] elements occurred in higher [illegible] grown on cryptobiota [illegible] suggest that even [illegible] crusts sometimes [illegible] elements. [illegible] growth was [illegible] the soil

[illegible] Australia [illegible]

for a treatment in which the surface 1.0 cm of cryptobiotic crust was scalped away. Each species was seeded on 10–22 randomly chosen plots through a template at 32 locations per 1.0-m^2 plot. After the first growing season four of the five species had more seedlings on plots where the cryptobiotic crust was left intact; in total there were slightly over three times as many seedlings on the average crusted plot as on the average scalped plot. After three years a larger percentage of the seedlings survived on crusted than on scalped plots for all five species tested.

In Nevada, Eckert et al. (1986) planted seeds of six species on three types of surfaces: (1) those covered by a sparse plant litter cover and beneath a shrub canopy, (2) polygonal patterned surfaces covered by a vigorous growth of cryptogamic cover, and (3) polygonal patterned surfaces with little cryptogamic cover and in interspaces between shrubs as was surface type [illegible] of the six species tested established as [illegible] the type 2 surface as on other surface [illegible] even better on type 2 surfaces; the [illegible] established best on type 3 surfaces

TABLE 5. Percentage of the root length colonized by rhizosymbionts on cyanobacterial crusted or comparable soils without a biotic crust. Roots of five randomly chosen plants were examined per species and soil surface condition. The effect of cyanobacterial crusts (treatment) on amount of colonization of roots by rhizosymbionts is significantly positive (F-value for ANOVA = 7.94, $p < .01$, d.f. = 1). F-value for species effects was 8.26 ($p < .01$, d.f. = 5). *Plantago patagonica* was omitted from the latter analysis.

Species *	Associate microbe	No biotic crust	Cyanobacterial crust
		- - - - - Avg. percent of root length colonized - - - -	
Bromus tectorum	VA mycor.[1]	3	8
Coleogyne ramosissima[2]	VA mycor.	5	18
Festuca octoflora	VA mycor.		
Colorado Plateau		T	1
Washington County		2	4
Lupinus pusillus	*Rhizobium*	22	34
Plantago patagonica	VA mycor.	No sample	13
Stipa hymenoides	Rhizosheaths[3]	40 (all weak)	100 (60% strong)

*Roots of the following species were studied, but no mycorrhizae were observed: *Cryptantha pterocarya*, *Cryptantha crassisepala*, *Mentzelia albicaulis*, and *Streptanthella longirostris*. All of these species are annuals.

[1] Vesicular arbuscular mycorrhizae

[2] Only seedlings arising from rodent caches were examined for this species.

[3] Rhizosheaths are dense tangles of root hairs, cells of a *Bacillus polymyxa*-like bacterium capable of N-fixation, and adherent sand grains (Wullstein and Pratt 1981).

and did poorly on type 2 surfaces. Lesica and Shelly (1992) reported that cryptogamic soil surface cover appeared to increase survival of established plants of *Arabis fecunda* Rollins (Brassicaceae) in Montana.

The foregoing reports suggest that establishment and survival of seed plants native to arid lands may often be enhanced by cryptobiotic cover on soil surfaces. As Harper and Marble (1988) show, several scientists have successfully used inocula of cyanobacteria to increase establishment and growth of agricultural crops in various parts of the world. Accordingly, observations of positive interactions between cyanobacterial-rich crusts and seedling establishment and growth in natural arid land environments are not surprising.

Although the influence of cyanobacterial-rich soil crusts on essential mineral uptake by associated seed plants appeared to be strongly beneficial for N only, there is reason to believe that enhanced tissue content of N, Ca, Mg, Na, and P may be beneficial to associated herbivorous and granivorous animals. Robbins (1983) notes that increased dietary protein consistently hastens growth and onset of reproductive maturity in herbivorous animals. Cyanobacterial crusts consistently increased protein content of associated shallow-rooted seed plants and seedlings of deeper-rooted plants in this study (Tables 2, 4; Belnap personal communication). Aumann (1965), Aumann and Emlen (1965), Belovsky (1981), and Robbins (1983) suggest that sodium in plant tissues is often inadequate to maintain healthy herbivores. Robbins's (1983) review of dietary sodium requirements for animals suggested that diets with less than 500 ppm sodium will eventually result in poor growth or death of animals. We note that cyanobacterial crusts always enhanced plant tissue content of Na in this study (Tables 2, 4). In our study, however, even plants grown on crusts did not contain the recommended minimum content of Na. Thus, animals must resort to local "mineral licks" to obtain adequate Na. Such licks may be widely spaced on sandy uplands such as those sampled for this report. Small mammals such as the granivorous heteromyid rodents common on deserts considered here may be especially dependent on Na in plant tissue, since they defend small territories that would rarely include a lick where supplementary minerals could be acquired. In such cases, increased tissue content of Na in plants growing on cyanobacterial-rich surface crusts may be of critical importance to associated heteromyid rodents.

Robbins (1983) considered that "calcium deficiencies are probably the major mineral problem encountered in captive wildlife." He noted that Ca and P are major constituents of the vertebrate skeletal system. In mature animals, 90% of Ca and 80% of P occur in bone, which has a Ca:P ratio of about 2:1. Since these elements are so intricately associated in bone, they are often discussed together. Birds use Ca not only in bone but also in eggshells, which are 98% $CaCO_3$ and less than 1% P. Osteoporosis is related to deficiencies in Ca and/or P in the diet or to major imbalances in their presence in the food base. Osteoporosis has been reported for free-ranging carnivores in Alaska, for reindeer on lichen-dominated ranges, and for the desert tortoise, a herbivore, from the warm deserts of southwestern Utah (Jarchow 1987, Robbins 1983). Carnivores may be especially prone to osteoporosis since flesh contains little calcium. Osteoporosis in the desert tortoise is surprising; Jarchow (1987) considered the disease to be a principal cause of death for the tortoise in Utah. He found the onset of osteoporosis to be premature and pathogenic in the animals examined. No disease could be shown to be associated with osteoporosis; thus Jarchow (1987) concluded that the condition was caused by dietary deficiencies. Since the principal food plants taken by the tortoise in southwestern Utah (Hansen et al. 1976) do not appear to be deficient in Ca (Jarchow 1984), the limiting element is probably P. Jarchow's (1984) and our own data (Tables 2, 4) both show less P in plant tissue than is considered necessary by Robbins (1983).

Since growth on cryptobiotic crusts has been observed to increase plant tissue content of P in *Festuca octoflora* (Table 2), *Coleogyne ramosissima* seedlings, *Lepidium montanum* var. *jonesii* (Belnap personal communication), and *L. montanum* var. *montanum* (Marble 1990), and to have no effect on tissue P content in *Streptanthella longirostris* (Belnap personal communication), it seems possible that cryptobiotic crusts could affect dietary intake of P by the desert tortoise. Since our data show that P is also occasionally [illegible] in plants growing on cyanobacterial [illegible] *Mentzelia* in Table 2 and [illegible] 4), more research is needed [illegible] spread coverage of [illegible] or decrease [illegible] Its much [illegible] as endangered [illegible]

Masslich 1985), and their importance in those environments is also known to have been severely depleted by uses imposed by European man (Anderson et al. 1982, Callison et al. 1985). Restored vigor of those crusts may improve dietary quality for desert tortoises.

Although Robbins (1983) concluded that Mg rarely poses a dietary problem for herbivores, Grunes et al. (1970) and Fairbourn and Batchelder (1980) suggest that less than 0.25% Mg in the forage base puts ruminant animals at risk for grass tetany, a nutritional disease resulting in vasodilation, hyperirritability, and muscle damage, and possibly culminating in paralysis and death. Magnesium is an essential element for proper bone and tooth formation and is an important enzyme activator for all animals. Absorption of Mg by the digestive organs is apparently inhibited by high levels of N and K in the forage; thus, grass tetany is most often observed when animals are feeding on lush spring growth of grasses. We note that Hansen et al. (1976) found that annual grasses make up 68% of the desert tortoise's diet in southwestern Utah. Our data show that cryptobiotic crusts consistently enhanced Mg content of tissue of associated plants (Tables 2, 4). We suggest that the influence of cryptobiotic crusts on Mg in plants eaten by the desert tortoise merits further attention.

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EFFECTS OF RANGEFIRE ON SOIL ALGAL CRUSTS IN SEMIARID SHRUB-STEPPE OF THE LOWER COLUMBIA BASIN AND THEIR SUBSEQUENT RECOVERY

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ABSTRACT—Effects of rangefire on soil algae in sagebrush steppe in the Lower Columbia Basin were studied. Dynamics of recovery of the soil algal community in the first two years following the fire were also documented. The study site was on the Arid Lands Ecology Reserve managed by Battelle Pacific Northwest Laboratory. Fire decreased the numbers of algae by more than an order of magnitude. Species composition in burned plots was similar to that in unburned plots, although some cyanophyte algae, particularly *Nostoc commune*, were decimated by the fire. Algal recovery took place in the winter months of the second year. Ninety taxa of algae were identified during the course of the study, over half of which were chlorophytes. Seasonal changes in the algal flora were also noted.

Key words: algae, soil; cryptogamic crusts; microbiotic crusts, rangefire, seasonality; Microcoleus vaginatus; Nostoc commune; *Arid Lands Ecology Reserve.*

Several researchers have claimed that cryptogamic soil crusts are critically important components of the arid and semiarid lands in which they occur (Harper and Marble 1988, Metting 1991). Cryptogamic crusts, or microbiotic crusts, are thought to stabilize the soil surface and thus reduce erosion due to wind and thunderstorms. They may also contribute to soil fertility through nitrogen fixation, organic carbon contributions, and accumulation of soil fines. Some evidence indicates the crusts may increase vascular seedling establishment (St. Clair et al. 1984). Water relations of the soil are also affected in a complex way, and the crusts may or may not improve water relations for vascular plants. Many of those who consider crusts valuable are particularly concerned about the destruction of crusts by grazing livestock, off-road vehicles, foot traffic, and rangefire.

However, some workers have challenged the majority opinion that cryptogamic crusts are important in the ecosystems in which they occur (West 1990, Gutknecht 1991). West has been particularly critical of those claiming crusts are of utmost importance, questioning the methodology of other workers and calling for more research before conclusions are made as to their relative value. Other workers, such as Savory (1988), are of the opinion that soil crusts are actually undesirable elements of the ecosystem and advocate range management practices that disrupt the continuity of the crust.

To resolve the controversy over the potential roles that cryptogamic crusts play in their environment, more research is needed on their long-term effects on stabilization of soil surfaces, contribution to soil fertility, and interaction with the vascular plant communities in which they occur. We also need to know more about the effects of various forms of disturbance on the crusts and the details of their recovery following such disturbance.

This paper reports the effects of rangefire on the soil algal communities of a sagebrush steppe and documents the first two years of recovery following the fire. The work was undertaken to fill two major gaps in our understanding of cryptogamic crusts. First, past studies (Johansen et al. 1982, 1984) have looked at recovery 3–5 years after the fire rather than immediately following the event. Initial effects of rangefire and early recovery stages have to this point been unknown. Second, most studies of cryptogamic crusts in the United States have been conducted in the Great Basin and Colorado Plateau provinces (see Harper and Marble 1988, Metting

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[illegible]

[illegible] Soil characteristics of burned and unburned [illegible] samples collected 28 September 1984. Each [illegible] represents a mean of 3 samples. The overall mean for [illegible] is given. There were no significant differences [illegible] soil parameters according to Student's t test [illegible]

Characteristic	Burned	Unburned	Mean
Percent sand	18.6	20.2	19.4
Percent silt	56.8	56.5	56.6
Percent clay	24.6	23.3	23.8
Percent organic matter	1.57	1.05	1.30
Percent organic carbon	0.91	0.61	0.76
Soil pH	6.49	6.47	6.48
Phosphate µg/g	10.6	7.7	8.2
Potassium µg/g	379	280	330
Nitrate-N µg/g	3.7	0.5	2.1
Ammonium-N µg/g	2.58	1.23	1.91
Sulphate µg/g	10.0	8.3	9.2
Bulk density	1.07	1.14	1.10
Conductivity µS/cm	61.0	55.0	58.0

[illegible] and West 1990 for extensive reviews of these studies). Although other studies of soil algae have been conducted in the Northwest (Fairchild and Willson 1967, Metting 1980, Metting and Rayburn 1979, Rayburn et al. 1982, Zimmerman et al. 1980), this study represents the first quantitative investigation of soil algae from crusted soils of the shrub-steppe region of the Columbia Basin.

SITE DESCRIPTION

The Arid Lands Ecology (ALE) Reserve is [illegible] the Hanford Reservation in the [illegible] Columbia Basin near Richland, Washington. The Hanford Reservation, set aside in [illegible] agriculture, grazing, and [illegible] (Thorp and Hinds [illegible] has altered the [illegible] consisting [illegible]. Although soil [illegible]

Pursh) Gould, *Festuca ovina* L., and *Poa secunda* Presl. Without grazing pressure, sagebrush has been slow to reestablish itself in these burned areas.

On 10 August 1984 a major rangefire burned an area of over 200,000 acres (most of the ALE Reserve). The fire burned both shrubland and grassland. In an area near ALE headquarters a sagebrush locality was burned unevenly, leaving several unburned sagebrush islands. A pair of transects was established in one of these unburned sagebrush islands, with a similar pair established in the burned field nearby. The study area has an aspect of about 4°, with drainage to the northeast into Cold Creek Valley. Soil at the study site is a Ritzville Silt Loam (Thorp and Hinds 1977).

MATERIALS AND METHODS

A pair of parallel transects 1 m apart with a total of 15 permanent points, each 1 m distant from adjacent points, was placed in one of the sagebrush islands. A similar pair of transects, also with a total of 15 permanent points, was established in an adjacent burned area about 6 [illegible] from the sagebrush island. The points were [illegible] with red surveyor's tape tied to large [illegible]. On each sample date two shallow soil cores [illegible] from each point. Since sampling was [illegible] samples were taken from previously [illegible] as close to the point as possible. [illegible] for each site was determined on [illegible] date by collecting soil samples in cans from the middle of each pair of transects (3 replicates/site until 17 June 1985, 10 replicates thereafter). Samples were taken 15 times in two years on the following dates: 9/28/84, 11/26/84, 2/25/85, 4/14/85, 6/17/85, 8/22/85, 9/28/85, 11/8/85, 1/23/86, 2/27/86, 3/28/86, 5/8/86, 5/30/86, 7/31/86, and 9/12/86.

Samples were taken using 1.9-cm-diameter sterile stainless steel cylinders with removable steel caps (Rayburn et al. 1982). In the field the cores were pushed into the ground to remove a relatively undisturbed core of soil. One set of 30 cores was used to make dilution plate cultures; the other set was processed using a technique we call the moistened soil method.

To make dilution plate cultures, the cores were returned to the laboratory, the caps removed, and the soil pushed up through the core with a wooden dowel. The top few millimeters were removed with an alcohol-sterilized razor blade and placed in tared, sterile flasks. An attempt was made to remove 1.0–1.5 g of soil in this fashion from each of the 30 cores. Then sterile distilled water was added to each flask to bring the soil/water weight to 100 g. The flasks were placed in a Burrell wrist-action shaker for 30 minutes to loosen the crust.

Tenfold dilutions were made and 0.1-ml aliquots were plated, three plates per dilution, on soil extract agar (Starr 1978). Incubation conditions were 21°C and 175 $\mu E\ m^{-2} s^{-1}$ irradiance from cool-white fluorescent lamps regulated on a 16:8 h L:D cycle. Viable counts of algae were made after 10–20 days of incubation. Generally 10^3 dilution plates were used, but in instances in which there were more than 300 colonies per plate, 10^4 dilution plates were used instead.

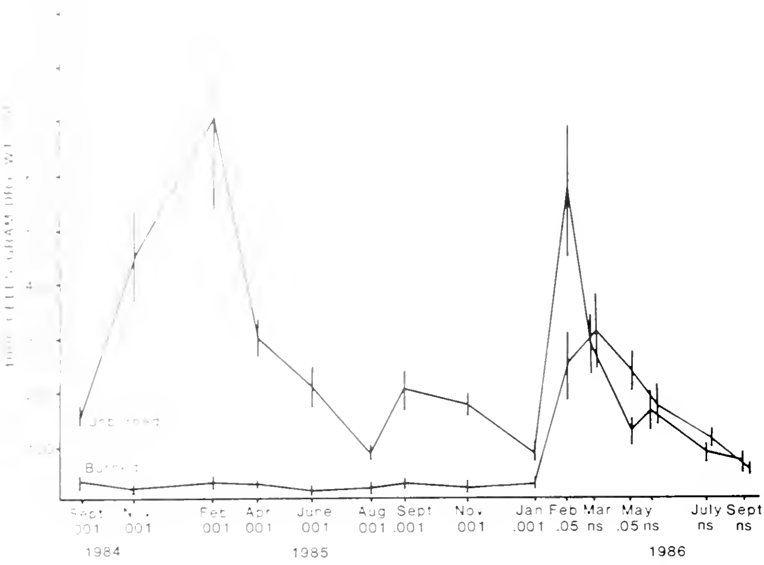
Following enumeration, algal isolations were made from the agar dilution plates into Bold's basal medium (Bold 1949) modified by the addition of 40 ml soil water extract/liter. On each sampling date about 100 isolations were made. Many of these isolations were found to be multiple isolations of the same species, but by isolating such a large number of algae, many of the more rare forms were also collected. Algal isolates were identified using a number of taxonomic references, of which the most valuable were Desikachary (1959), Ettl (1978), Ettl and Gaertner (1988), Geitler (1930–1932), Komarek and Fott (1983), and Starmach (1972). We were able to identify most isolates at least to the generic level, but on every sampling date there were some isolates for which no determination could be made. These few representatives were omitted from the analyses reported in this paper. Isolations were made only during the first year of the study.

The other 30 cores were processed using the moistened soil method. This method is described in detail in Johansen et al. (1984), but we will briefly review it here. For each sample, 2.5–3.0 g of soil were placed in a sterile petri dish and flooded with sterile distilled water. The petri dishes were incubated under controlled conditions at 22°C on a 16:8 h L:D cycle for 8 days. Frequency and relative abundance of living algae were estimated by subsampling the center of each petri dish and examining this subsample under the light microscope. A total of 50 microscope fields were examined for each subsample, and the presence or absence of each species in each field was noted. The moistened soil method was used because in past instances we found it more effective for enumeration of cyanobacteria than the dilution plate method. This method was employed only during the first year of the study.

On each sample date a kodachrome slide of each sample point was taken to chronicle the recovery of the vascular plant flora. Cover of grasses, forbs, shrubs, and cryptogamic crusts was estimated for all sample plots in the months of April (spring) and September (late summer).

Six months into the study we realized that patterns of algal abundance in the burned plots were apparently related to patterns of fire intensity in the burn. Using the photographic record of the sites, we calculated a burn intensity index (BI) by calculating the sum of scores for each of the following five characteristics: (1) blackening of the soil (0 = none, 1 = ≤30% of plot, 2 = >30%), (2) grass sprouting from crowns (0 = >10, 1 = 1–10, 2 = none), (3) living moss cover (0 = >5%, 1 = 1–4%, 2 = <1%), (4) crust cover in February 1985 (0 = >50%, 1 = 20–50%, 2 = <20%, and (5) crust cover in June 1985 (0 = >50%, 1 = 20–50%, 2 = <20%). The index ranged from 0 (very lightly burned) to 10 (intensely burned). The variation in intensity was apparently due to the fact that grasses and forbs did not burn as hotly as shrubs. The scores for the burn index are given in Table 1.

Nitrate nitrogen, ammonium nitrogen, sulphate, phosphate, potassium, percent organic carbon (Walkley-Black method), and percent organic matter were determined for samples



[illegible] M[illegible] [illegible] densities of burned and unburned transects as determined using the dilution plate technique. Error [illegible] [illegible] ANOVA was performed to compare the burned and unburned means on each sample date; [illegible] F tests are listed below sample month designations.

[illegible]ected on 28 September 1984 by the Soil Testing Laboratory, University of Idaho in Moscow, Idaho. Soil texture (gravimetric method), pH, electrical conductivity, and bulk density were determined by the authors following standard methods (Soil Conservation Service 1972, Soil Survey Staff 1962). For all analyses, [illegible] replicate samples were analyzed from [illegible] plot. Results of these analyses are [illegible] Table 2.

Several different biometric methods were [illegible] the data. Analysis of variance was [illegible] algal abundance for each [illegible] and Casella 1980). This [illegible] data (algal density [illegible] algal frequency [illegible] principal [illegible] dilution plates, we were unable to conduct PCA on that data set. However, we were able to cluster the samples using Sorenson's similarity index and the unweighted group average method (Pielou 1984, Sorensen 1948).

Data from both methods did not appear to form a normal distribution. Data from the moistened soil method were particularly suspect because of the high number of zero frequencies in the samples. Thus, Pearson's r (based on the normal distribution) was deemed inappropriate. Where measurement of correlation between samples was needed, the nonparametric Kendall rank correlation test was used (Sokal and Rohlf 1981).

All analyses were conducted using either the Statgraphics statistical package or the Ecology Program Library developed by Bill Evenson and Jack Brotherson at Brigham Young University (unpublished).

RESULTS

[illegible]nounced differences existed between the [illegible] and unburned sites throughout the first [illegible] study. Algal density as determined [illegible] dilution plate technique revealed pro[illegible] seasonal changes in unburned plots [illegible] the study, with a major peak in late winter and a minor peak in the fall (Fig. 1). Mean algal density for unburned plots ranged over 1–7 × 10^5 cells/g dry weight soil. Considerable variability among samples within unburned transects was evident. The range for algal density for all samples taken from the unburned area was 10^3–2.7 × 10^6 cells/g. Algal density in the burned area did not show seasonal changes or recovery for the first 16 months after the fire (Fig. 1). Mean algal density during this period had a range of 2–3.5 × 10^4 cells/g, with individual sample ranges of 10^3–1.3 × 10^5 cells/g. Recovery of the algal community in the burned plots occurred during the winter months of the second year in a very short time frame (January to March). Analysis of variance for each sample period showed significant ($p < .05$) differences between burned and unburned transects through February 1986, after which the burned area had similar or greater numbers of algae than the unburned area (Fig. 1).

No statistically significant differences in algal density using the moistened soil method were found between burned and unburned transects, although both blue-green algae and diatoms had higher mean frequencies in unburned plots (Fig. 2). Some of the samples in the burned area had algal frequencies of zero, while others had frequencies similar to those in unburned plots. Considerable variability was observed in unburned plots as well. It is likely that this heterogeneity in both burned and unburned plots contributed to the non-normality of the data and is thus responsible for the lack of power of the statistical procedure used. When the data were transformed using a $\log_{10}(x + 1)$ transformation, significant ($p < .05$) differences were detected for some dates (9/84, 2/85, 6/85, 9/85). Because of the lack of significant differences, the moistened soil method was discontinued after the first year. It is interesting to note that the method did locate seasonal differences in the burned area comparable to those seen in the unburned area (Fig. 2).

When first visiting the site, we were struck by the fact that the algal/moss crust, though blackened and dead, was still very much intact. If this phenomenon occurs elsewhere, we surmise that crusts may be important in stabilizing soils of burned areas during the critical period when all vascular vegetation is absent and soil is exposed to the full erosive forces of wind and water. The blackened crust slowly broke down over the first 6–8 months after the rangefire, at which time visible vascular recovery had occurred.

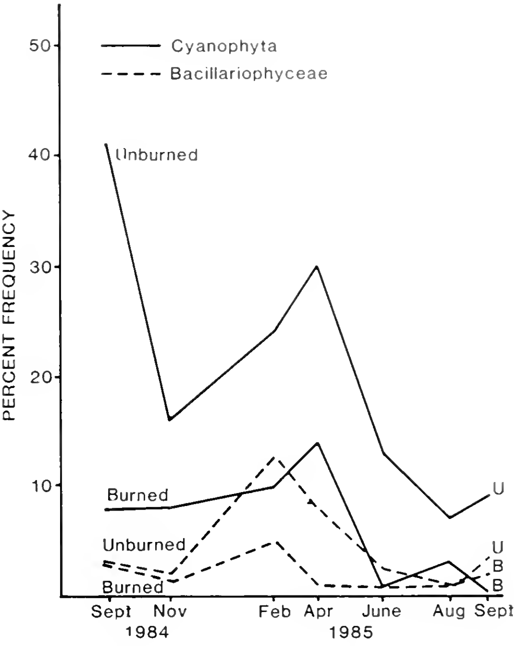


Fig. 2. Mean percent frequencies of blue-green algae (Cyanophyta) and diatoms (Bacillariophyceae) as determined using the moistened soil method. Standard error bars are not included because in all cases they overlapped. ANOVA did not reveal any significant differences.

Some areas in the burned transects seemed to be less damaged than others. This was especially noticeable after fall rains in 1984 stimulated some of the burnt grasses to sprout back from the crowns. There were areas where grasses had sprouted back profusely and crusts were intact and unblackened, areas where fewer grasses sprouted and the crust appeared damaged but not excessively blackened, and areas where no grasses sprouted and blackened crusts already had begun eroding. Upon investigating the transects closely, we found burnt remnants of sagebrush stems in the heavily burned plots. It was evident that any place a sagebrush burned, the fire was much hotter in intensity, causing destruction of both grasses and crusts in close proximity.

With such evident differences in fire intensity, we checked to see whether algal numbers reflected these differences. We found a striking correspondence. Kendall's rank correlation of the burn intensity index (BI) with algal density (dilution plate method) was consistently negative [illegible] Kendall [illegible] for all sample dates. Correlation values with the burn intensity [illegible]

[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	8/85	9/85	11/85	1/86	2/86	3/86	5/86	5/86	7/86	9/86	BI
[illegible]	[illegible]	[illegible]	[illegible]	.19	.20	[illegible]	.39	.40	.17	.02	.27	−.28	.44°	.33	−.03	−.50°
[illegible]		1.00	[illegible]	[illegible]	[illegible]	.71	.10	.27	.20	.12	.29	−.18	.28	.06	−.24	−.66°
[illegible]			1.00	[illegible]	[illegible]	.35	.03	.42	.18	.11	.20	−.29	.14	.05	−.08	−.37°
[illegible]				1.00	[illegible]	[illegible]	.18	.28	.39°	.16	.16	−.56°	.40°	−.03	−.04	−.36
[illegible]					1.00	.19	.12	.39	.27	.08	.13	−.32	.22	.04	−.20	−.48°
[illegible]						1.00	.01	.20	.14	.15	.42	−.14	.22	.10	−.24	−.59°
[illegible]							1.00	.41	.57°	.05	.11	−.06	.43°	.30	.10	−.43°
[illegible]								1.00	.54	.11	.28	−.12	.33	.24	.12	−.36°
[illegible]									1.00	.16	.20	−.17	.62°	.41°	.23	−.45°
[illegible]										1.00	−.03	−.06	.10	.01	−.31	−.02
[illegible]											1.00	.02	.31	−.07	.08	−.44°
[illegible]												1.00	−.18	.10	.13	.10
[illegible]													1.00	.27	.39°	−.54°
[illegible]														1.00	.21	−.28
[illegible]															1.00	−.04

[illegible] significant (p [illegible] .05) during the first 16 months of the study (Table 3), indicating that the more intense the fire (higher BI), the lower the algal density. Especially surprising was the persistence of patterns of algal abundance through the full two-year study. When contour plots based on algal density were constructed, it was [illegible] that areas of high algal density remained [illegible] throughout the study (Fig. 3). On most [illegible] there is an area of higher abundance [illegible] middle of the left hand transect [illegible] sample plots 27, 29 [illegible] had the lowest BI values [illegible] BI values (plots 16, 17 [illegible] lower left, respec- [illegible] densities [illegible] soil [illegible] high densities on the second date and plots with low densities on the first date had low densities on the second date. In the first year's data (9/84–8/85) all sample dates were positively correlated with all other dates, with 8 of 15 (53%) of these correlation coefficients being statistically significant (Table 3). The plots were shifted the second year to avoid the area that had been destructively sampled the first year. During the second year (9/85–9/86), 78% of the correlation coefficients were positive, with only 25% of these being statistically significant. These results indicate that the pattern caused by initial fire intensity was strong throughout the first year but began to break down when algal recovery took place in the winter of the second year (from 2/86 to the end of the study).

Similar patterns in algal density were sought in the unburned transects. However, the heterogeneity of the unburned area was so great that no such patterns could be detected in contour plots. Kendall rank correlation coefficients between all sample dates for unburned plots showed much less correlation than that seen in the burned plots. Although most of the coefficients for the first year's data were positive, only

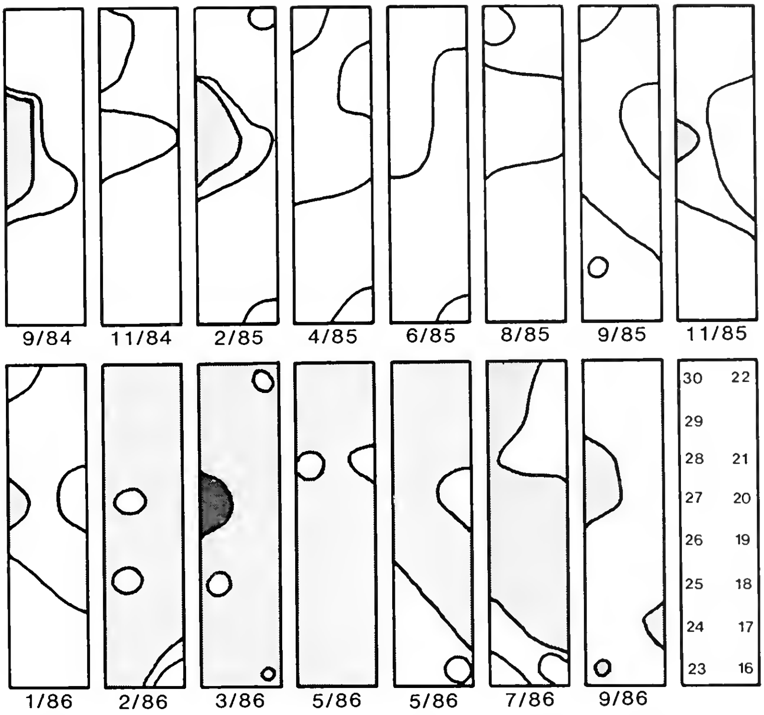


Fig. 3. Algal densities for the burned transect as determined using the dilution plate technique. Last box shows plot positions during the first year (see Table 1). White represents $<2 \times 10^4$ cells/g, light shading represents $2\text{–}10 \times 10^4$ cells/g, medium shading represents $10^5\text{–}10^6$ cells/g, dark shading represents $>10^6$ cells/g.

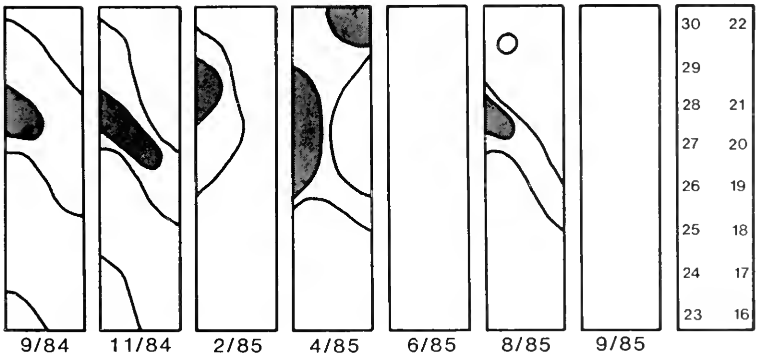


Fig. 4. Blue-green algal percent frequencies as determined using the moistened soil method. Last box shows plot positions (see Table 1). White represents 0–4%, light shading represents 5–29%, dark shading represents 30–100%.

3 of 15 (20%) were significant (Table 4). During the second year only 69% of the coefficients were positive, with 3 of the 36 (8%) being statistically significant. With an alpha level of 0.05, one would expect "significant" coefficients 5% of the time simply by random chance. The ratio of 7 of 105 correlation coefficients in Table 4 is very close to this hypothetical 5%, and we suspect this may mean that no meaningful patterns were detectible with our sampling design. This suggests that extensive microscale heterogeneity is present in the microbial distribution of undisturbed arid soils, a topic that has been subsequently pursued by others (Grondin and

[illegible] computed [illegible] for all sample dates.

	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	11/85	1/86	2/86	3/86	5/86	5/86	7/86	9/86
[illegible]	[illegible]	[illegible]	[illegible]	11	00	25	06	06	23	16	07	−.10	03	−.07	−.09
[illegible]		[illegible]	06	07	01	21	24	19	09	17	25	17	−.21	−.08	−.04
[illegible]			1.00	17	02	29	10	16	15	22	33	.14	.12	−.12	.05
[illegible]				1.00	16	20	07	17	05	14	06	10	.15	−.04	−.20
[illegible]					1.00	15	12	02	09	15	33	.06	27	.08	.10
[illegible]						1.00	28	10	16	06	19	15	.38*	15	.30
[illegible]							1.00	08	03	13	−.15	.08	11	−.11	−.14
[illegible]								1.00	19	45*	16	20	.22	.05	.07
[illegible]									1.00	29	10	−.06	.10	00	14
[illegible]										1.00	.18	−.01	01	−.05	−.01
[illegible]											1.00	.35	.37	−.03	14
[illegible]												1.00	.18	.16	14
[illegible]													1.00	26	43*
[illegible]														1.00	.47*
[illegible]															1.00

[illegible] ALL plots based on cultures obtained from agar plates. B = burned, U = unburned, C = 0% [illegible] stand for months from September 1984 to September 1985.

	S/C	N/B	N/U	F/B	F/U	A/B	A/U	J/B	J/U	A/B	A/U	S/B	S/U
[illegible]			X				X						
[illegible]					X	X	X	X		X	X		X
[illegible]						X	X	X	X	X	X		
[illegible]		X	X	X		X		X			X		
[illegible]		X			X	X	X	X	X				
[illegible]	X			X	X	X	X		X		X		X
[illegible]							X	X			X		
[illegible]			X							X	X		X
[illegible]				X	X	X	X	X	X				X
[illegible]	X	X	X		X					X	X		
[illegible]	X		X		X		X		X		X		X
[illegible]				X	X	X	X		X		X	X	X
[illegible]	X	X		X	X		X						
[illegible]		X	X	X	X	X			X				X
[illegible]			X	X	X	X	X	X	X	X	X		X
[illegible]		X	X	X	X	X	X			X	X	X	X
[illegible]					X	X	X			X			
[illegible]									X				
[illegible]				X					X		X		
[illegible]			X	X	X	X		X	X		X	X	X
[illegible]				X	X	X		X					
[illegible]						X							
[illegible]									X		X		X
[illegible]					X		X	X	X		X	X	X

TABLE 5. Continued.

Species	SC	NB	NU	FB	FU	AB	AU	JB	JU	AB	AU	SB	SU
Chlorococcum arenosum Archib. & Bold	X	X	X	X	X	X	X		X	X	X	X	X
Chlorococcum infusionum (Schrank) Menegh				X									
Chlorococcum minutum Starr			X		X	X	X	X					
Chlorosarcina sp. 1	X	X	X		X	X			X	X	X		X
Chlorosarcina sp. 2						X							X
Chlorosarcinopsis sp						X		X	X				X
Chlorozebra cohaerens Vinatzer	X			X	X	X		X					X
Fasciculochloris sp.		X	X	X	X		X				X	X	X
Follicularia sp. (?)											X		
Fottea sp.				X	X								
Friedmannia israelensis Chant. & Bold	X	X	X	X	X		X					X	
Gloeocystis polydermatica (Kuetz.) Hind.			X	X	X	X	X		X		X		
Leptosira polychloris				X		X	X	X	X	X	X		X
Leptosira sp.									X		X		
Lobococcus incisus (Reisigl) Reisigl	X								X				X
Lobococcus macronucleatus (Deason) Bourr.				X									
Myrmecia bisecta Reisigl				X		X	X		X	X	X	X	X
Neochloris sp. 1						X					X		
Neochloris sp. 2						X							
Neospongiococcum ovatum Deason								X					
Neospongiococcum sp. 1		X	X	X	X					X	X	X	X
Neospongiococcum sp. 3					X	X	X		X		X		
Palmella miniata var. *aequalis* Naeg. sensu Smith							X						
Palmella texensis Groover & Bold	X	X	X	X	X		X	X		X	X		X
Pleurastrum sp. 1	X	X	X	X	X	X	X	X	X	X	X		X
Pleurastrum sp. 2					X	X		X		X	X		
Protosiphon sp.				X	X	X	X	X	X	X	X		X
Radiosphaera minuta Herndon	X			X									
Spongiochloris sp.					X								
Stichococcus bacillaris Naeg.	X			X		X		X	X	X			X
Stichococcus minutus Grintzesco & Peterfi				X	X	X	X		X				X
Tetracystis sarcinalis Schwartz							X	X	X		X		
Tetracystis sp.			X	X	X		X		X				X
Trebouxia sp.				X	X		X			X	X		X
Trichosarcina sp.		X			X								
Chlorosarcinoideae sp.	X				X		X	X	X	X			X
XANTHOPHYCEAE													
Ellipsoidion anulatum Pascher				X			X	X			X		X
Ellipsoidion oocystoides Pascher	X	X	X	X	X	X	X	X	X		X	X	X
Ellipsoidion perminimum Pascher				X		X					X		
Gloeobotrys ovalis Reisigl					X								
Heterococcus granulatus Pitschmann					X								
Heterothrix debilis Vischer	X			X	X	X	X			X		X	X
Nephrodiella phaseolus Pascher							X	X	X			X	X
Pleurochloris commutata Pascher	X	X		X				X			X		
Pleurochloris meiringensis Vischer					X								
BACILLARIOPHYCEAE													
Hantzschia amphioxys (Ehr.) Grunow	X	X	X	X	X	X	X	X	X	X	X		
Navicula mutica Kuetzing				X	X		X	X		X	X		
Pinnularia borealis Ehrenberg			X		X			X	X	X	X		

Johansen 1993, Wheeler et al. 1993). Correlations of algal density with vascular cover were also attempted without success.

A total of 72 algal taxa were isolated from the soils at ALE over the course of the two-year study (Table 5). Over half the isolations were green algae (47 taxa), with blue-green algae (13 taxa) being next in importance. Additional blue-green and diatom taxa were observed by using the moistened soil method (Table 6). In all, 47 Chlorophyta, 26 Cyanophyta, 9 Xanthophyceae, and 8 Bacillariophyceae were observed, for a total of 90 taxa. This may be the highest diversity of algal species ever reported from soils of a [illegible] AEF plots using the moistened soil method. B [illegible] burned, U [illegible] September 1984 to September 1985.

	S/B	S/U	N/B	N/U	F/B	F/U	A/B	A/U	J/B	J/U	A/B	A/U	S/B	S/U
[illegible]		1.9												0.7
[illegible]								1.2				0.1		
[illegible]			0.3	2.7										
[illegible] Gom.		0.1	0.3	0.7					0.7	1.1	0.5	0.9	0.1	
[illegible]														0.3
[illegible]			0.1											
[illegible]														0.3
[illegible]		0.1	0.1											
[illegible]	0.5	2.9	0.1	0.1	0.8	3.1	2.0	4.5	0.3	1.7				0.1
[illegible] Gom.	1.9	3.5	1.3	0.7	6.4	1.6	9.7	10.9	0.3	0.8	1.7	1.1		0.4
[illegible]	0.1	21.2	0.1	3.7	0.1	7.1	1.2	5.6	0.1	7.6	0.5	5.4		5.3
[illegible]		2.4	0.3	0.7	0.1	0.1	0.3	0.4		0.3	0.2			1.6
[illegible] Gomont	0.1	0.8	1.1	1.2	0.1	0.3		0.1		0.1				0.1
[illegible] Koppe	0.5	2.8		0.1	1.2	8.9	0.1	0.8		0.3				
[illegible] Gom.		0.5				0.3		0.1				0.1	0.1	
[illegible]	2.9	5.2	3.9	5.1	0.4	2.3			2.1	3.7	1.2	1.6		
[illegible] Menegh. Gom.			0.4	0.1	0.5	0.4	0.5	2.0		1.1	0.2	0.4	0.1	0.3
[illegible] Naeg.	0.8	0.5			0.1						0.2			
[illegible] Breb & Desm. Forti									0.7				0.4	
[illegible] Kuetz. J. Schmidt		0.9		1.3		0.1	0.1	1.0				0.1		
[illegible]	7.6	41.5	8.0	16.4	9.9	21.3	14.0	29.7	3.8	17.3	2.6	7.4	0.4	9.5
[illegible]														
[illegible] Brebisson							0.1							
[illegible]					0.4								0.5	0.1
[illegible] Ehr. Grunow	0.5	1.1	0.3	0.9	2.3	7.1	0.3	2.1	0.5	0.4		0.3	0.9	0.3
[illegible] Hilse Grun.								0.1			0.2		0.1	
[illegible] Kuetzing	0.6	0.4	0.1		0.8	1.0	0.3	0.5	0.1	0.4	0.3		0.9	
[illegible] Hilse Grun.							0.3							
[illegible] Ehrenberg											0.2			
[illegible] Ehrenberg	[illegible]	1.6	0.9	1.1	0.9	2.6		1.7		1.2		0.1		1.3
[illegible]	[illegible]	3.4	1.2	2.0	4.0	10.7	0.7	7.7	0.7	2.0	0.8	0.4	1.6	2.7
[illegible]	78.7	26.8	11.1	32.7	94.5	62.0	70.7	62.4	17.6	26.5	22.0	18.4	105	85.5

[illegible] One likely explanation for the num- [illegible] observed is the extended period [illegible] taken and the sheer [illegible] performed. The fact that [illegible] employed also con- [illegible] richness. [illegible] differences [illegible] burned and un- [illegible] observed [illegible] D. Because of time constraints, algal isolations were not made after the first year.

The results of both the dilution plate technique and moistened soil method indicate that significant differences existed between the algal communities until the winter months of the second year, when rapid recovery occurred. We were interested in documenting floristic patterns of recovery as well. Using data from the moistened soil method, we computed Ruzicka's similarity coefficients and produced a dendrogram describing the cluster of the communities (Fig. 5). Four cluster groups were identified.

Only unburned communities are in the first cluster. Based on the results in Table 6, all of [illegible] communities are characterized by having [illegible] numbers of *Nostoc commune* Vaucher and

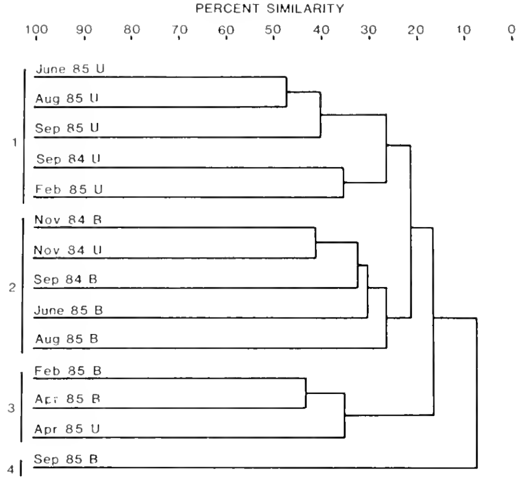


Fig. 5. Cluster dendrogram based on Ruzicka's similarity index using quantitative data from the moistened soil method. The first cluster contains unburned communities, the second burned communities, the third represents a seasonal spring flora, and the last cluster is an outlier due to the near absence of species observed in September 1985. See text for further explanation.

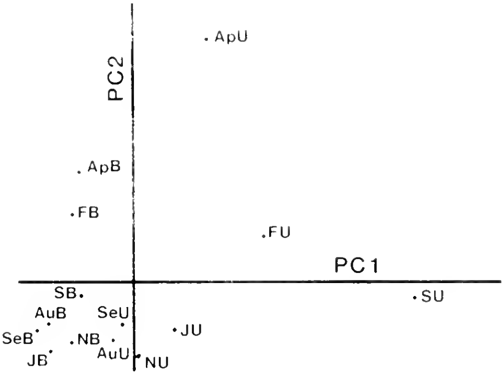


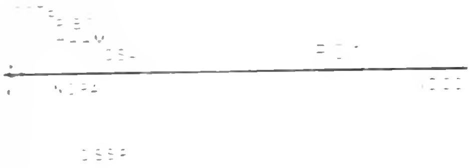
Fig. 6. Plot of the first and second components from an unstandardized, centered principal components analysis of data collected using the moistened soil method. Codes represent date (S = 9/84, N = 11/84, F = 2/85, Ap = 4/85, J = 6/85, Au = 8/85, Se = 9/85) and transect (B = burned, U = unburned); i.e., ApU = 4/85 unburned transect.

low numbers of *Microcoleus vaginatus* (Vauch.) Gomont. The second cluster contains mostly burned communities, although the November unburned community is present because of its similarity to the November burned community. This cluster is characterized by low numbers of both *N. commune* and *M. vaginatus*. Thus, it appears that *Nostoc* species were damaged by the fire and did not recover during the first year. The third cluster represents seasonal changes in *M. vaginatus*, which had elevated numbers in the early spring samples. The last cluster consists of a single outlier, the September 1985 burned community. This sample is distinct in that both *N. commune* and *M. vaginatus* are absent (Table 6).

Principal components analysis (PCA) of the same data set corroborates and further clarifies the cluster analysis. Principal component 1 reflects the differences due to burning. Collectively, the unburned floras have higher scores on PC axis 1 than all burned floras (Fig. 6), although some unburned floras are close to the relatively tight cluster of burned floras. When each date pair is examined, the unburned flora has a distinctly higher score on PC axis 1 than its corresponding burned flora. The second PCA axis seems to reflect seasonal influences, with late winter/early spring floras having higher scores.

When the component weights are plotted, it is evident that PC axis 1 is most heavily weighted by numbers of *N. commune*, indicating that this species is the primary contributor to the separation of burned and unburned floras (Fig. 7). Nearly all species are weighted positively because average algal densities for all species tended to be higher in unburned plots. PC axis 2 is most heavily weighted by *M. vaginatus* (Fig. 7), the taxon that separates late winter/early spring communities from the rest of the year's samples. Principal components 1 and 2 explain 56% and 24% of the variability in the data, respectively.

Since we do not have quantitative information for individual species identified from isolations, we could not perform PCA or cluster analysis based on Ruzicka's similarity index. However, Sorenson's similarity index could be calculated, and cluster analysis based upon this similarity coefficient was performed (Fig. 8). The first cluster consists of communities with high numbers of taxa and comprises late winter–late spring unburned samples, as well as the February burned community. The second cluster is not separate from the first but is hierarchical to it. This part of the cluster consists of the communities that had slightly lower species richness and hence lower similarity. The late summer community from unburned transects also was in this group, indicating that some species diversity may be lost in the summer even in undisturbed areas. The third cluster consists



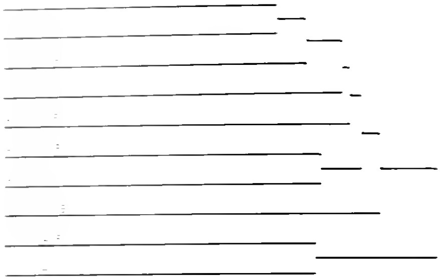


TABLE 7. Vascular plant cover observed in the burned and unburned transects at the ALE site (%). Data from late summer and spring for each year of the study is presented.

	9/84		4/85		9/85		4/86		9/86	
Cover class	B	U	B	U	B	U	B	U	B	U
Artemisia tridentata Nutt.		0.2		T		5.[illegible]		4.8		7.2
Poa secunda Presl		22.7	8.6	58.1	7.[illegible]	49.[illegible]	15.[illegible]	70.[illegible]	2[illegible]	47.[illegible]
Other grasses			0.4		0.2		[illegible]	[illegible]		
Lupinus leucophyllus Dougl.			0.3		0.7		[illegible]1.4	2	[illegible]	[illegible]
Other forbs			0.7	0.9	0.9		[illegible]	[illegible]7	2	[illegible]
Total vascular cover	0.0	22.9	10.0	59.0	9.7	54.4	4[illegible]	[illegible]4	28.4	7[illegible]4
Total crust cover	80.3	71.9	52.6	63.5	64.5	50.[illegible]	58.7	4[illegible]	44.[illegible]	4[illegible]
Bare ground	19.7	5.4	37.7	1.[illegible]	25.6	T	20.4	2[illegible]	27.7	[illegible]
Litter	T	5.6	0.9	3.8	0.7	7.8	0.2	[illegible]7	[illegible]	2.5

ᵃT = trace

bination of factors limited growth during the first year.

Three factors are most likely responsible for this phenomenon. While physical soil characteristics and chemistry were not significantly ($p < .05$) different between sites (Table 2), it is possible that hydrophobic organic compounds released by the fire sealed the soil surface, causing greater runoff and less water availability. Light burning on dry soils has been demonstrated to produce a thick and highly water-repellent soil layer in California chaparral soils (DeBano et al. 1970, 1976). The pH did not change following burning, which was unusual since in most instances pH increases following fire (Groeschl et al. 1991, McKee 1991). Nitrate nitrogen increased immediately following the fire (Table 2), but it may have subsequently decreased. Soil nitrogen dynamics associated with fire are poorly understood and a topic of vigorous debate by others (Klopatek et al. 1991, McKee 1991). However, it is unlikely that nitrogen availability explains the failure of algal populations to grow the first year.

A second possibility is that algae require a vascular plant canopy for development. Vascular plant cover in the burned area was completely destroyed by the fire (Table 7). Some grasses sprouted from crowns in late fall of 1984, and by spring of 1985 grass cover in the burned area was about one-sixth of that in the unburned area. Upright forbs did not appear until the summer of 1985 and were more abundant in burned transects than in the unburned island (Table 7). It seems plausible that vascular cover would ameliorate harsh conditions of sun and wind on the soil surface, thus promoting algal growth. Standing vegetation in the winter, even if dead, could prolong periods of optimal soil moisture at the soil surface and could have contributed to recovery during the second winter.

A third possibility is that the wetter winter of 1985–86 was partly responsible for algal recovery. Johansen et al. (1984) surmised that unusually wet weather was largely responsible for algal recovery in a burned site studied in Utah. A comparison of precipitation for the two winters shows that over twice as much precipitation fell the second winter (Fig. 9). For the months of December to March, 12.0 cm precipitation fell the second year, compared with 5.3 cm precipitation the first year. Furthermore, air temperatures were above freezing between January and March when recovery occurred, whereas 1984–85 temperatures had been consistently below freezing (Fig. 9).

We are unable to say which of the three factors discussed above played the most significant role in algal recovery. It is likely that some combination of these and possibly other factors is responsible. More research on cryptogamic recovery following disturbance is needed. At the same time, it should be recognized that recovery following fire is likely very different from recovery following trampling disturbance (livestock, off-road vehicles) because of the differences of impacts on soils and vascular communities.

We observed clear evidence of seasonality in algal abundance at the ALE site. A repeating pattern of winter and fall peaks was observed using the dilution plate method. Seasonality was not limited to density differences; floristic changes also occurred. When algae identified from isolations were clustered using Sorenson's similarity quotient, November floras of burned and unburned transects clustered together (Fig. 8). August floras also formed a distinct cluster. The two February floras clustered together

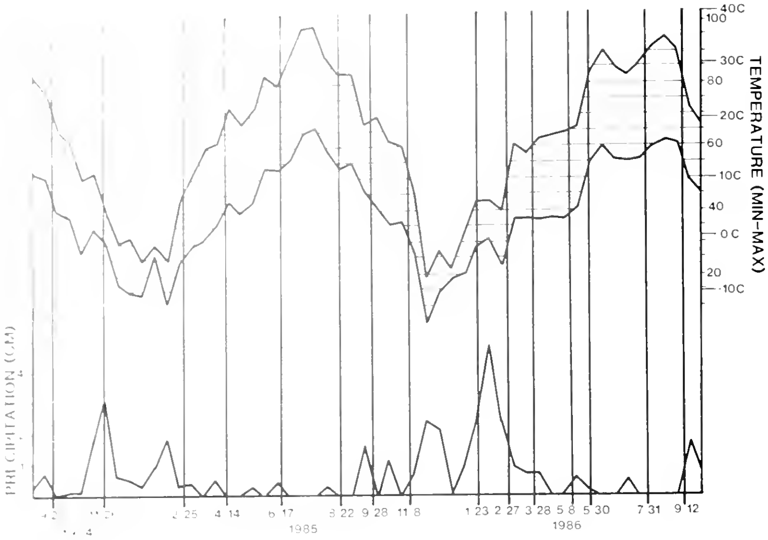


Fig. [illegible]. Climate diagram for the ALE site for the duration of the study. The temperature range represents the mean minimum and maximum temperature based on two-week periods. Precipitation represents the total precipitation over the same periods. Vertical lines represent sample dates.

along with the unburned April community. The tendency for floras to cluster by season rather than treatment reflects the importance of seasonality even when a crude measure such as presence/absence of taxa is considered. The data obtained using the moistened soil method gave a clearer indication of seasonal change. Specifically, *Microcoleus vaginatus* and diatoms showed high abundance in the early spring months of February and April (Table 6). *Chroococcus* spp. were absent during the early spring months, and *Nostoc commune* was highest in September 1984 in the unburned transect (Table 6).

Seasonality of algae of arid soils was studied by Johansen and Rushforth (1985). Their results [illegible] as the results in this [illegible] November and June. [illegible] greatest abundance [illegible] Unfortunately, they [illegible] and May the [illegible] ALE site. Further [illegible] Uinta Moun[illegible]

result of dense tree canopy and shading by leaf litter (Grondin 1991). The presence of seasonality in desert soils raises concerns about the methods of study employed by past workers. In a number of studies samples have been collected only once during the year, based on the assumption that a single collection is representative of the site in terms of numbers and species present (Anderson and Rushforth 1976, Ashley et al. 1985, Cameron 1960, Fairchild and Willson 1967, Johansen and St. Clair 1986, Johansen et al. 1981, 1982, 1984). Our data show this assumption is erroneous. Finally, although difficult to study, seasonality requires closer examination if an understanding of long-term succession is eventually to be gained.

The algal flora of the ALE site in the Lower Columbia Basin is distinctively different from floras reported from shrub-steppe communities of the Great Basin and Colorado Plateau. The major difference is the high diversity and abundance of green algae and xanthophytes in the ALE soils. A total of 47 chlorophytes and 9 xanthophytes were observed at a single site. In most previous studies these algae have not been identified even to generic level (Anderson and Rushforth 1976, Ashley et al. 1985, Johansen and St. Clair 1986, Johansen et al. 1981, 1982, 1984). In a study of over 450 specimens of soil from seven counties in Arizona, Cameron [illegible] reported only 12 chlorophytes and 1 xanthophyte. One possible explanation for the abundance of these algae at ALE is that the soil pH is slightly acidic, whereas almost all arid shrub-steppe soils studied in the Great Basin, Colorado Plateau, and Sonoran Desert are slightly to strongly alkaline. In studies of the relationship of soil pH to algal floras, both John (1942) and Lund (1947) found that acid soils support more green than blue-green algae. Other studies of Washington soils have had high numbers of chlorophytes compared to cyanophytes (Metting and Rayburn 1979, Rayburn et al. 1982, Zimmerman et al. 1980). Fairchild and Willson (1967) found a pronounced effect of soil pH in their study of soil algae in arid Washington soils, with a higher chlorophyte/cyanophyte ratio in neutral soil than in the alkaline soil they studied. More study of chlorophytes and xanthophytes in alkaline soils of the Great Basin and Colorado Plateau is warranted.

Although by comparison blue-green algae seemed scarce, the diversity of cyanophytes observed was also higher than in most previous studies. For example, the maximum number of cyanophyte species reported from studies of Great Basin and Colorado Plateau soils is 17 (Anderson and Rushforth 1976, Ashley et al. 1985, Johansen and St. Clair 1986, Johansen et al. 1981, 1982, 1984), compared with the 26 taxa observed in the present study. In a study of arid soils of neutral to alkaline pH in the Lower Columbia Basin, Fairchild and Willson (1967) found 20 species of blue-green algae, which is comparable to the number observed in this study when one considers that they sampled only in the spring months.

Results of this study have raised as many questions as they have answered. Algal recovery time, density, and species composition observed at the ALE Reserve suggest much greater regional differences in cryptogamic crust biology than previously assumed. Because of the constancy in macroscopic appearance and the presence of some ubiquitous taxa, such as *M. vaginatus*, *N. commune*, and *Hantzschia amphioxys* (Ehr.) Grunow, some workers may have considered soil algal communities of arid lands fairly similar. This perception is flawed, and more study of diverse arid localities is needed. Furthermore, the lack of standard methodologies for the study of soil algae and cryptogamic crusts has made comparison between studies very difficult. Further study of the chlorophytes and xanthophytes is probably warranted, as is continued study of seasonality. Sampling once a year should be considered insufficient in future studies. And, finally, although recovery from fire requires (in many cases) two to five years, more study is needed regarding the dynamics of recovery in different types of shrubland and in different climatic regimes. The complexity of soil algal communities emerging as a result of numerous unrelated studies should continue to confuse and delight researchers for years to come.

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RECOVERY RATES OF CRYPTOBIOTIC CRUSTS: INOCULANT USE AND ASSESSMENT METHODS

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ABSTRACT—Recovery rates of cyanobacterial-lichen soil crusts from disturbance were examined. Plots were either undisturbed or scalped, and scalped plots were either inoculated with surrounding biological crust material or left to recover naturally. Natural recovery rates were found to be very slow. Inoculation significantly hastened recovery for the cyanobacterial/green algal component, lichen cover, lichen species richness, and moss cover. Even with inoculation, however, lichen and moss recovery was minimal. Traditional techniques of assessing recovery visually were found to underestimate time for total recovery. Other techniques, such as extraction of chlorophyll *a* from surface soil and measurement of sheath material accumulation, were used and are discussed

Key words: cyanobacteria, soil algae, cryptobiotic crusts, cryptogamic crusts, recovery, disturbance, reclamation, innoculation, Microcoleus vaginatus.

Cyanobacterial soil crusts occur in semiarid and arid regions throughout the world. Studies of these crusts have documented the importance of the role they play in these ecosystems. This role includes the stabilization of soils (Belnap 1990, Harper and Marble 1988, Marathe 1972), improved nutrient status of vascular plants growing in the crust (Belnap and Harper unpublished), and improved soil structure (Metting and Rayburn 1983).

For the National Park Service, maintaining the biota and visual aesthetics of undisturbed landscapes is a central concern. Since cryptobiotic crusts are widespread throughout parks on the Colorado Plateau and damage to them is highly visible, finding methods to hasten the recovery of disturbed crusts is of importance to this agency. The use of inoculants to speed up recovery of these crusts has been reported by several authors (Ashley and Rushforth 1984, Lewin 1977, St. Clair et al. 1986, Tiedemann et al. 1980).

Traditionally, assessment of recovery rates of cryptobiotic soil crusts after disturbance has been based on visual measurements only. Generally, such measurements have included percent cover of the cyanobacterial/green algal, lichen, and moss components; presence of pediceled soil surfaces; and number of moss and lichen species observed (Anderson, Harper, and Holmgren 1982, Anderson, Harper, and Rushforth 1982, Brotherson et al. 1983, Cole 1990). Unfortunately, visual measurements cannot quantify the amount of the cyanobacteria/green algae present, since filaments and cells ramify through several millimeters of surface soils. The few studies that have attempted to quantify the amount of cyanobacteria and green algae tissue present have used fluorescence optics or culturing (Ashley and Rushforth 1984, Johansen and Rushforth 1985). Both methods have problems associated with them: fluorescence optics is very time consuming, and culturing may give misleading results. Recently, Beymer and Klopatek (1992) used chlorophyll *a* to estimate cyanobacterial and green algal tisue in recovering crusts.

Another aspect of crust recovery should also be considered. *Microcoleus vaginatus*, the cyanobacterium that makes up the bulk of crustal organisms in the semiarid environments considered here, may contribute up to 95% of the crust biomass (Belnap personal observation). This cyanobacterium secretes a thick, extracellular gelatinous sheath around the living filaments. This sticky sheath material adheres to soil particles, thereby aggregating them into larger, less erodible particles (Belnap and Gardner 1993, Harper and Marble 1988). When moistened, the filaments of *Microcoleus* are partially extruded from the colonial sheaths; the filaments

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[illegible] and [illegible] the abandoned sheath material behind. Consequently, there is much more abandoned than currently inhabited sheath material in a well-developed crust (Belnap and Gardner 1993). Since abandoned sheath material still adheres to and binds together soil particles, it continues to contribute to soil stability and may increase moisture and nutrient retention in these soils (Belnap and Gardner 1993). Thus, any assessment of recovery of crusts should consider the amount and condition of both abandoned and occupied sheath material present.

The purpose of this study was twofold. The first was to establish whether inoculation using nearby biotic crustal material could be used to increase biotic recovery rates of disturbed crusts. The second was to examine other methods of assessing crust recovery. These included (1) using chlorophyll *a* to quantify living cyanobacterial/algal components of the crusts, (2) measuring height of biologically induced microrelief, and (3) assessing accumulated sheath material.

METHODS

Studies were conducted on sandy and gypsiferous substrates. Plots were established in four places: (1) on a gypsiferous substrate in Arches National Park (ARCH), about 20 miles northwest of Moab, Utah, in 1988; (2) on a sandy substrate at Sand Flats (SF), 5 miles east of Moab in 1987; (3) on a sandy substrate in the Behind the Rocks (BTR) area, 10 miles south of Moab in 1985; and (4) on a sandy substrate at the Island-in-the-Sky (ISKY) district, Canyonlands National Park, about 20 miles northwest of Moab in 1988. At the ARCH and ISKY sites, [illegible] plots were randomly assigned to one of [illegible] disturbed or undisturbed, and [illegible] (ARCH) and 5 (ISKY) times. The [illegible] consisted of scalping the [illegible]. Half of the disturbed sites were [illegible] for inoculation. Inoculation [illegible] the scalped material [illegible] the mixture [illegible] chlorophyll *a* [illegible]. At the [illegible] [illegible] BTR [illegible] were 0.25 m² in area, three were 0.5 m², and two were 0.75 m².

Sites were sampled in 1990. Since plots were established at various times during the 1985–88 period, different recovery periods were represented. Gypsiferous plots at ARCH and sandstone plots at ISKY were sampled after two years, SF plots were sampled after three years, and BTR sites were sampled after five years. Measurements consisted of 5–10 samples of crust (cores 1 cm deep by 1.6 cm in diameter) collected from each plot. Chlorophyll *a* in these samples was extracted with dimethyl sulfoxide (DMSO); this extract was centrifuged and spectrophotometrically analyzed at an optical density of 665 nm.

Visual estimates of cryptobiotic cover were taken at all sites as well. Percent cover of cyanobacteria/green algae, mosses, and lichens was recorded for all treatments at all sites. Height of pedicellation (measured from the highest point of the pedicel to the ground surface between pedicels) and thickness of the crust (depth to which the sheaths of *Microcoleus* could be detected) were measured at the BTR site. Thickness of the crust was measured by slicing through the crust with a razor blade. In the coarse, sandy soil found at the BTR site, sand not bound by gelatinous sheath material fell away freely, enabling one to estimate the depth to which sheath material was present.

Data were analyzed for significance using an unpaired Student's t test to compare inoculated with uninoculated plots; ANOVA and Duncan's multiple range test were used to distinguish significant differences between uninoculated, inoculated, and control plot values. Each characteristic was run separately (chlorophyll *a*, lichen and moss cover, and richness). Probabilities of $<.05$ were considered statistically significant.

RESULTS

All parameters measured for all treatments at all sites were statistically different ($p < .001$) except for the visual assessment of cyanobacterial/green algal cover. For this characteristic all surfaces at all sites appeared to be 100% covered within a year. In uninoculated plots the cyanobacterium *Microcoleus vaginatus* was always the first to develop observable cover. In all disturbed plots where any lichens were observed, the lichen *Collema tenax* was always present.

TABLE 1. ARCH site: average values for selected parameters of cryptobiotic crusts following various treatments. Recovery interval was 2 years. See text for details of treatments and biotic variables. All differences are statistically different at the $p < .05$ level, except moss cover (all values zero).

	Absorption by chlorophyll *a*		Lichen cover		Lichen species		Moss cover	
Treatment	$\bar{X}$	S.D.	$\bar{X}$	S.D.	$\bar{X}$	S.D.	$\bar{X}$	S.D.
Control	0.14	0.03	43.3	12.1	4.3	0.3	0.0	0.0
Inoculated	0.08	0.02	3.6	2.9	2.6	0.5	0.0	0.0
Uninoculated	0.03	0.001	1.3	1.5	1.8	0.4	0.0	0.0

TABLE 2. BTR site: average values for selected parameters of cryptobiotic crusts following various treatments. Recovery interval was 5 years. See text for details of treatments and biotic variables. All differences are statistically different at the $p < .05$ level.

	Absorption by chlorophyll *a*		Lichen cover		Lichen species		Moss cover	
Treatment	$\bar{X}$	S.D.	$\bar{X}$	S.D.	$\bar{X}$	S.D.	$\bar{X}$	S.D.
Control	0.09	0.07	23.2	3.0	4.4	0.9	11.6	3.2
Uninoculated	0.01	0.01	0.0	0.0	0.0	0.0	0.0	0.0

Arches

Plots at this site were scalped and either inoculated with nearby biotic crustal material or not inoculated. Chlorophyll *a* and visual characteristics were measured after two years. All biotic aspects of recovery on this gypsiferous substrate were significantly enhanced by inoculation, including chlorophyll *a* concentrations, percent cover of lichens, and number of lichen species present (Table 1). Chlorophyll *a* in undisturbed crusts was almost twice that of inoculated plots (0.14 vs. 0.077), and almost five times that of uninoculated crust (0.14 vs. 0.03). Lichen cover averaged 43.3% on undisturbed plots, 3.6% on inoculated surfaces, and 1.3% on uninoculated surfaces (all differences are statistically significant). Lichen species on undisturbed areas averaged 4.3 per plot, while on the inoculated surfaces this average was 2.6. Uninoculated surfaces averaged 1.8 species per plot. No mosses were present on any surfaces. The only exception to these significant differences between treatments was the visual assessment of the cyanobacterial/green algal cover. All treatments gave the appearance of 100% coverage within one year.

Behind-the-Rocks

Plots at this site were either scalped or left undisturbed. No plots were inoculated. Measurements were taken five years later. After this time period all parameters measured showed large and statistically significant differences between the undisturbed and uninoculated, scalped areas (Table 2). Visually, the scalped areas looked well on their way to recovery. The entire surface area of scalped plots appeared covered by cyanobacteria, and pedicellation had begun. Pedicel height in undisturbed crusts ranged from 4.3 to 7.9 cm, averaging 4.9 cm. In scalped plots, pedicels averaged 2 cm in height, or about 41% of the average pedicel height on undisturbed plots. From this, one might assume that the cyanobacterial/green algal component was 41% recovered. However, chlorophyll *a* levels and the thickness of sheath accumulation necessitate a different interpretation. Chlorophyll *a* levels were still only 12% of those in undisturbed sites after five years. Measurements of depths to which accumulated sheath material could be detected demonstrated that on scalped plots, though pedicels averaged 2 cm in height, thickness of sheath material was only 0.6–0.9 cm, averaging 0.8 cm. Over half the volume of the average pedicel consisted of loose [illegible] of cryptobiotic crusts following various treatments. Recovery [illegible] variables. All differences are statistically different at the p

	Absorption by chlorophyll *a*		Lichen cover		Lichen species		Moss cover	
	$\bar{X}$	S.D.	$\bar{X}$	S.D.	$\bar{X}$	S.D.	$\bar{X}$	S.D.
[illegible]	[illegible]	0.02	7.3	3.4	0.9	0.3	7.3	3.4
[illegible]	[illegible]	0.01	1.8	1.8	0.7	0.5	1.2	1.5
[illegible]	[illegible]	0.001	0.3	0.5	0.3	0.5	0.0	0.0

[illegible] for selected parameters of cryptobiotic crusts following various treatments. Recovery [illegible] See text for details of treatments and biotic variables. All differences are statistically different at the p

[illegible]	Absorption by chlorophyll *a*		Lichen cover		Lichen species		Moss cover	
	$\bar{X}$	S.D.	$\bar{X}$	S.D.	$\bar{X}$	S.D.	$\bar{X}$	S.D.
[illegible]	0.3	0.05	42.5	12.9	4.3	1.1	12.1	10.5
[illegible]	0.02	0.001	1.5	1.1	1.1	0.6	0.09	0.3

sand. On the other hand, in undisturbed plots sheath material occurred throughout the volume of the pedicels, and little loose sand was found. In the undisturbed crust sheath material was observable at an average depth of 4.9 cm, or six times the depth measured in the scalped areas. The difference was highly significant statistically.

Lichen cover showed no recovery at all: while undisturbed sites averaged 23.2% cover, no lichens were found in the scalped plots after [illegible]. An average of 1.1 lichen species were found on the undisturbed plots, while none were found in the scalped plots. Moss cover [illegible] no recovery, though undisturbed [illegible] 11.6% moss cover (Table 2).

[illegible]

[illegible] and then either [illegible] material or [illegible] measurements [illegible] levels [illegible] differ [illegible] areas averaged 7.3%. Inoculated plots had significantly less lichen cover (1.8%), and uninoculated plots averaged 0.3% lichen cover. The same pattern was observed for moss cover: undisturbed plots averaged 7.3%, inoculated plots averaged 1.2%, while uninoculated plots had no moss cover at all. Visual assessment of the cyanobacterial/green algal cover was rated as 100% after one year for all treatments.

Sand Flats

Plots at this site were either scalped or left undisturbed, with measurements taken three years later. As with the other sites, all parameters were significantly different between scalped and undisturbed plots (Table 4). Chlorophyll *a* levels in the scalped areas were only 8% of those observed in the undisturbed areas (0.022 vs. 0.275) after three years. Reestablishment of lichens was again exceptionally slow: after three years, scalped plots had only 1.5% lichen cover compared to 42.5% cover found in nearby undisturbed areas. Scalped plots averaged only 1.0 lichen species per plot, while undisturbed areas averaged 4.3. Moss cover was slow to recover as well. While undisturbed areas had an average of 12.1% cover, the disturbed areas averaged 0.09% cover. As with the other areas, visual assessment of cyanobacterial/green algal cover reached 100% within one year.

DISCUSSION AND CONCLUSION

It is clear from these results that inoculation can hasten the biological recovery of disturbed crusts. Inoculated plots had far greater chlorophyll *a* concentrations than uninoculated plots, indicating a larger establishment of cyanobacteria and green algae. They also had significantly greater lichen species richness and greater lichen and moss cover than uninoculated plots. It should be noted, however, that although lichen cover and moss cover were significantly greater on inoculated than uninonculated plots, recovery for both lichens and mosses was extremely slow for both treatments.

Inoculation hastened some aspects of visual recovery of the cyanobacterial/green algal component. Areas that had been inoculated had greater pedicellation sooner than areas that were not inoculated. Apparent coverage of the soil surface by this crustal component, however, was not hastened by inoculation, since all soil surfaces appeared completely covered within one year. Inoculation somewhat hastened the visual recovery of the lichens and mosses; however, absolute differences were so small that it was difficult to tell treatments apart without close examination.

The use of spectrophotometrically determined chlorophyll *a* in surface soil as a measure of recovery of cryptobiotic crusts proved to be a time-efficient and reliable measure. When comparing different treatments or areas, however, one must take all samples within a short period of time to eliminate seasonal variations in chlorophyll *a* as a potentially confounding variable.

Visual assessment as a means of determining crust recovery proved to be misleading. All plot surfaces, whether inoculated or not, appeared completely covered by cyanobacteria, and most showed rudimentary pediceling after only one year. This gave the impression that the cyanobacterial/green algal components of the crusts were mostly or fully recovered. Chlorophyll *a* measurements, however, told a different story: dramatic differences in chlorophyll *a* levels demonstrated that the amount of photosynthetic cryptobiotic tissue present differed greatly among treatments. Uninoculated plots sometimes supported only 2% as much chlorophyll *a* as was found in nearby undisturbed crusts. Visual assessment also did not accurately assess the accumulation of abandoned sheath material. The method employed in this study to measure the gelatinous sheath material accumulated was not completely satisfactory in that it worked well only in dry, coarse-grained soils. Some other means of assessing this crustal characteristic must be developed to be used on all types of substrates. This assessment should take into account both the amount of polysaccharide material present as well as its structural integrity. The bulk of microbiotic tissue in sandy soils consists of abandoned, buried sheath material. Though abandoned, this sheath material probably reduces soil erodibility and enhances moisture and nutrient retention of the soil. Any damage to such abandoned material, however, is non-repairable, since living filaments are no longer present to re-secrete the gelatinous material. Repeated trampling of this brittle material pulverizes the abandoned sheaths, breaks up their connections to sand grains, and probably hastens aggregate dissolution. For this reason, assessment of recovery from disturbance should consider not only the presence of living organisms and the amount of abandoned sheath material present, but also the integrity, or condition, of the sheath material. In places where all or most sheath material has been removed (such as construction sites), assessment of crustal integrity and depth is much simplified. However, in situations where sheath material is repeatedly trampled in place, quantification of the crustal condition is much more difficult. Chemical analysis of sheath material will not give us information about the integrity of that material; yet quantification of integrity is critical to any assessment of crustal recovery and resultant stability of the system.

Prior estimates of time for natural recovery of cryptobiotic crusts from disturbance have varied widely, ranging from a few years to 100 years for full recovery of all components (Anderson, Harper, and Rushforth 1982, Callison et al. 1985, Cole 1990, Jeffries and Klopatek 1987, Johansen et al. 1982, 1984). In this study it is clear that if only visual estimates of cyanobacterial cover are considered, recovery appears quite rapid, whether sites are inoculated or not. This is generally supported by other studies that utilized visual assessments (Cole 1990, Johansen and Rushforth 1985), where recovery was reported in up to five years. However, there has been an exception—Johansen et al. (1984), who [illegible] however, [illegible] visual [illegible]

Other [illegible] recovery, such as chlorophyll *a* levels, [illegible] enumeration, depth ramified by thickness of accumulated sheath material, [illegible] lichen and moss species and [illegible] generally occur much more slowly (Anderson, Harper and Rushforth 1982, Callison et al. 1985, Harper and Marble 1988, Jeffries and Klopatek 1987, Johansen and St. Clair 1986). Chlorophyll *a* levels increased 1% a year at the ISKY site, while at other sites they increased approximately 2.4, 2.5, and 2.6% a year. Assuming a linear accumulation rate and the greatest rate of increase observed, full recovery of chlorophyll *a* levels would take about 40 years. At the BTR site depth ramified by sheath material ranged from 1.2 to 1.8 mm a year. If one assumes this accumulation process to be linear, and that temperatures and moisture conditions during the interval considered were fairly typical, recovery from disturbances that destroy accumulated sheath material may take longer. Attaining the average depth of ramification of surface soil observed here would take 30–40 years for full recovery. Maximum depths observed would require 40–65 years at the rates observed. Natural recovery rates of lichen and moss were much slower than those for cyanobacterial cover, chlorophyll *a* levels, or sheath depths. Lichens showed some recovery at three of the four sites. At observed rates full recovery at these three sites would take 45–85 years. At the BTR site no recovery was seen even after five years, and so time to full recovery is impossible to predict. Moss recovery was much slower than that of the lichens. At two of the three sites where mosses were found, no moss recovery at all was seen. [illegible] prediction of recovery rates impossible, [illegible] clearly these rates are extremely slow. [illegible] where some recovery was seen, [illegible] moss cover would take over 250 [illegible] rate of recovery. Recovery [illegible] crustal communities de[illegible] the type and extent of [illegible] time to recov[illegible] or infre[illegible] thereby [illegible] such as [illegible] rates [illegible] Johan[illegible] active when wet, years with higher effective precipitation will show faster recovery than years with lower effective precipitation (Belnap personal observation, Johansen et al. 1984, 1993). Different substrates (gypsiferous and sandy soils) did not affect recovery rates of cyanobacteria, mosses, or lichens in this study.

Much work remains to be done in the assessment of crustal recovery. Since recovery rates depend on type and extent of disturbance, availability of nearby inoculation material, and temperature and moisture regimes that follow disturbance events, the relative effect of all these factors must be better understood before managers can accurately estimate recovery rates at specific sites. In addition, more work is needed on ways to assess recovery, including linkage of chlorophyll *a* measurements and algal enumeration techniques, and inclusion of sheath integrity measurements. Also, more research should be directed at recovery rates for crusts on different substrates and with different floral compositions. This study demonstrates that recovery can take a long time, especially for lichen and moss components of cryptobiotic crusts. For this reason, a conservative approach should be adopted relative to activities that may disturb these crusts. More effort should be devoted to evaluating procedures that will hasten reestablishment of cryptobiotic crusts, such as inoculation with pulverized natural surfaces or artificially grown inocula.

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DEPLETION OF SOIL MOISTURE BY TWO COLD-DESERT BUNCHGRASSES AND EFFECTS ON PHOTOSYNTHETIC PERFORMANCE

Jay E. Anderson[1] and Nancee L. Toft[2]

ABSTRACT—This study compared the abilities of two cool-season bunchgrasses to extract moisture from a drying soil and compared photosynthetic and stomatal responses of the two species as soil moisture supplies were depleted. When grown in 49-L pots in a greenhouse, *Leymus cinereus* extracted more water from the soil and maintained higher gas exchange rates to lower absolute amounts of soil water than did *Agropyron desertorum*. The soil water content at the lower limit of extraction was 10.3% for *L. cinereus* and 13.3% for *A. desertorum*. When soil moisture was expressed as extractable soil water, there was little difference between the species in pattern of water use. Both species maintained high stomatal conductances (g_w) and photosynthetic rates (A) until extractable soil moisture was reduced to about 15%. For field-grown plants under severe water stress, A was higher in *L. cinereus* than in *A. desertorum* at comparable leaf water potentials. The relationship between A and g_w was similar for the two species; the higher A in *L. cinereus* was a consequence of higher g_w. Thus, higher A in *L. cinereus* is achieved through some sacrifice of water-use efficiency.

Key words: extractable soil water, leaf water potential, stomatal conductance, water-use efficiency, Leymus cinereus, Agropyron desertorum.

Plant species vary widely in their tolerance of seasonal drought and in the mechanisms they use to cope with declining supplies of soil moisture. Some species tolerate seasonal drought by maintaining high leaf water potentials through stomatal closure (Turner 1979). Although they may maintain a high photosynthetic capacity, low stomatal conductance will severely restrict carbon gain under prolonged drought. In contrast, other species allow their leaf water potentials to drop as soil water potentials decline (Turner 1979). This enables the plant to continue to extract water from a drying soil, but decreases in leaf water potential typically are accompanied by decreases in photosynthetic capacity and stomatal conductance (Jones 1973, Comstock and Ehleringer 1984, Ehleringer and Cook 1984, DeLucia and Heckathorn 1989, Chaves 1991) as well as changes in the diurnal patterns of gas exchange (Schulze and Hall 1982, Tenhunen et al. 1987). It clearly would be advantageous for such species to maintain photosynthetic rates as high as possible as soil and plant water potentials decline.

As plants extract water from a drying soil, the amount of plant-available water decreases exponentially with decreasing water potential (e.g., Slatyer 1967, Fig. 3.3). Consequently, the volume of water gained by a plant in drying a given volume of soil to −2.0 MPa over that gained in drying a soil to −1.5 MPa, for example, is so small that it would seem rather negligible in

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terms of total carbon gain. Jordan and Miller (1980) and Jordan et al. (1983) estimated that the additional water made available to a crop as a consequence of lowering leaf water potential "a few bars" would support transpiration only for 3 or 4 days in the absence of additional root growth. Thus, there would seem to be little advantage in making the necessary osmotic adjustment and/or other leaf modifications to tolerate very low water potentials, and we might expect little difference among drought-tolerant species in their lower limit of extraction of soil moisture. [We use Ritchie's (1981) definition of the lower limit of extraction: the amount of water remaining in the soil when plant growth and activity completely stop.]

On the other hand, tolerance of very low plant water potentials may offer advantages other than gaining more water from a particular volume of soil. Osmotic adjustment may enable a plant to maintain turgor in growing roots which, in turn, would enable the plant to explore the soil for additional water reserves (Sharpe and Davies 1979, Jordan et al. 1983, Westgate and Boyer 1985, Turner 1986). Drought-tolerant sagebrush (*Artemisia tridentata*) plants of the Great Basin of North America move water at night along a hydraulic gradient in the roots from deep in the soil to drier soil at shallow depths (Richards and Caldwell 1987, Caldwell and Richards 1989). The water deposited in those shallow layers can be extracted the following day to support carbon gain or other physiological activity. Finally, Caldwell (1985) postulated that drying a soil to a very low water content may be a way of excluding competitors. These arguments and results suggest that significant but possibly subtle differences could exist in the lower limit of extraction of soil water among species. Indeed, Sinclair and Ludlow (1986) found small differences in the lower limit of extraction among four tropical legumes grown in pots.

Anderson et al. (1987) compared the seasonal patterns of soil water extraction among four drought tolerant, cold-desert species. They found little difference in the lower limit of extraction among the four species when grown in monocultures on a common soil; however, there was some indication that the native bunchgrass *Leymus cinereus* (Scribn. & Merr.) A. Löve might be able to extract more water from a soil than could the introduced species *Agropyron desertorum* (Fisch. ex Link) Schult. In addition, preliminary gas-exchange data from field-grown plants (J. Anderson unpublished data) suggested that *L. cinereus* plants maintained higher photosynthetic activity and had higher stomatal conductance at low leaf water potentials than did *A. desertorum* plants. To test those possibilities, we conducted a greenhouse experiment (1) to compare photosynthetic and stomatal responses of these two species to drying soil and (2) to compare the lower limit of extraction of the two species. In addition, we compared photosynthetic capacity and conductance of the two species under water stress imposed naturally in the field. Both laboratory and field data support the hypothesis that, in comparison to *A. desertorum*, *L. cinereus* plants deplete soil moisture reserves more completely and maintain higher photosynthetic rates as water supplies are diminished; but this is achieved through some sacrifice in water-use efficiency by *L. cinereus*.

METHODS

Plant Materials

Leymus cinereus is a robust tussock grass native to cold deserts and lower mountain slopes throughout the Intermountain West of North America. It occurs on alkaline or saline lowland sites as well as nonsaline upland sites, often on deep soils (Young and Evans 1981, Walker and Brotherson 1982). Plants used in this study were transplanted from a near monocultural natural stand at the Idaho National Engineering Laboratory (INEL). Additional information concerning the ecophysiology of *L. cinereus* can be found in Anderson et al. (1993).

Agropyron desertorum is a tussock grass native to the steppes of Asia; it is naturalized in western North America, where it has been used extensively for rangeland rehabilitation. Stands established by seeding often persist as near monocultures (Marlette and Anderson 1986). Plants used in this study were transplanted from seeded stands at the INEL. Additional information about the ecophysiology of *A. desertorum* can be found in Nowak and Caldwell (1984, 1986) and Nowak et al. (1988).

Greenhouse Studies

Twenty-four pots were constructed from polyvinyl chloride pipes; each pot was 1 m tall and 0.25 m in diameter. The pots were filled with a 1:1:1 mixture of Baccto potting soil, sand, and a clay-loam soil used in experimental field plots at the INEL (see Field Studies). The mean (and standard error) dry mass of soil placed in the pots was 44.4 ± 0.4 kg. At field capacity that volume of soil held 18.5 ± 0.1 L of water, or 39.7% water by volume. Dormant *A. desertorum* and *L. cinereus* plants were collected from stands at the INEL in November and held at 5°C until 12 plants of each species were transplanted into the 49-L pots in December. The plants were placed in a greenhouse where they received natural sunlight supplemented by four 1500-W metal halide lamps. The height of the lamps was set so that photosynthetic photon flux density (PFD) at canopy height was 1500–2000 μmol m^{-2} s^{-1} at midday. The photoperiod was 13 h.

Plants were fertilized twice a week with full strength Ruakura nutrient solution (Smith et al. 1983). After the plants became well established, six of each species were assigned randomly to a well-watered (control) treatment, and the other six were assigned to a water-stress treatment. The well-watered plants received nutrient solution twice a week and distilled water once a week. Water stress was induced by withholding water from the plants for 50 days, after bringing the soil water content to field capacity. Because of the large volume of soil and water in a pot, water stress was imposed gradually, simulating soil drying that occurs naturally under field conditions.

The pots were weighed every 3–4 days during the drying period to determine the amount of water held in the soil of each pot. Soil water content was expressed in two ways. Percent of total soil water (TSW) was defined as (volume of water in the soil) / (volume of water at field capacity) × 100. Extractable soil water (ESW; see Ritchie 1981) was expressed as a percentage of the difference between the volumetric water content at field capacity and that when growth of that species had stopped (day 50 of the drying period). Soil water potential was measured with single-junction, screen-caged psychrometers (J. R. D. Merrill Specialty Equipment, Logan, Utah) placed at soil depths of 150, 350, 550, and 750 mm in three pots per species containing water-stressed plants. Psychrometric output was monitored every 3–4 days using a model NT-3 nanovoltmeter (Decagon Devices Inc., Pullman, Washington).

On day 33 there was a slight increase in the weight of pots in the water-stress treatment (Fig. 1), but it was not until we noted a substantial increase in weight of some pots on day 36 that we realized water had entered some pots from pools on the floor resulting from the watering of other plants. After day 36 the amount of water in the soil decreased to levels slightly lower than those on day 29. Because growth of individuals of both species had essentially stopped by day 33 and changes in soil water content after that date were negligible, only data for 33 days are included in most analyses presented here.

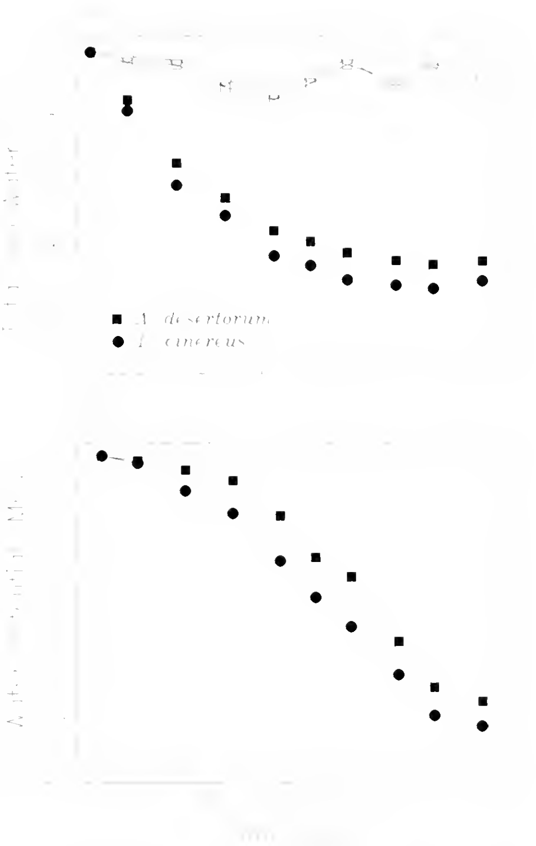

Fig. 1. (A) Changes in total soil water content with time after withholding water from *Agropyron desertorum* and *Leymus cinereus* plants (dashed lines) and for irrigated controls (solid lines) growing in 49-L pots in a greenhouse. (B) Soil water potential vs. time for treatment means corresponding to the closed symbols in A. See Table 1 for statistical analyses.

Rate of elongation of expanding leaves was used as an index of growth rate. Leaf elongation rate (LER) of the youngest leaf was determined by measuring its length at two times and dividing the difference in length by the time interval. Length measurements were made on two vegetative tillers per pot on three consecutive days each week. Leaf elongation rates reported here were averaged over 48 h.

[illegible] soil water content expressed as percent of total soil water, soil water content [illegible] leaf elongation rate of the youngest leaf on a tiller, and soil water potential for *Leymus cinereus* [illegible] plants growing in 49-L pots in a glasshouse. For each dependent variable, main effects were [illegible] interaction terms were not significant, they were excluded from the model. All independent variables [illegible] were treated as classification variables. There were two levels of species (SP: *A. desertorum* and *L. cinereus*). For all dependent variables in part a, there were two levels of stress (STR: well-watered and water-stressed) and 10 days (DAY) after water was withheld from the the water-stressed plants (1, 4, 8, 12, 16, 19, 22, 26, 29, 33). For soil water potential in part b, there were four levels of soil depth (DP: 150, 350, 550, 750 mm) and 9 days (DAY: 1, 8, 12, 16, 19, 22, 26, 29, 33).

Effect	Species	Stress	Day	SP × STR	SP × DAY	STR × DAY	SP × STR × DAY
Total soil water $n = 228$	$P < .0001$	$P < .0001$	$P < .0001$	$P < .0002$	–	$P < .0001$	–
Extractable soil water $n = 228$	n.s.[1]	$P < .0001$	$P < .0001$	–	–	$P < .0001$	–
Leaf elongation rate $n = 255$	$P < .0001$	$P < .0001$	$P < .0001$	$P < .0001$	$P < .0002$	$P < .0001$	$P < .0003$

b Effect	Species	Depth	Day	SP × DP	SP × DAY	DP × DAY	SP × DP × DAY
Soil water potential $n = 204$	$P < .002$	$P < .0001$	$P < .0001$	–	–	–	–

[1] n.s. = not significant

Field Studies

The field studies were conducted at the INEL Experimental Field Station where monocultures of *A. desertorum* and *L. cinereus* were established by transplanting mature individuals from nearby stands to experimental plots having a homogeneous soil to a depth of 2.4 m (see Anderson et al. 1987 for details). The soil consisted of 26% sand, 54% silt, and 20% clay and had a bulk density of 1.28 g cm^{-3}. The measurements reported here were made during the third growing season after the plants were transplanted.

Gas Exchange and Plant Water Potential Measurements

Net photosynthesis (A), transpiration (E), and leaf conductance to water vapor (g_w) were measured on the youngest, fully expanded leaves or on the penultimate leaf on a tiller after inflorescences developed, with an open, compensating gas-exchange system which has been previously [illegible] (Novak et al. 1988, Toft et al. 1989). [illegible] measurements of greenhouse-grown plants were made at a leaf temperature of [illegible], PFD of 1900–2000 µmol m^{-2}s^{-1}, and a leaf-to-air water vapor gradient (v) of 2 kPa. The concentration of CO_2 inside the cuvette was 330–340 µL L^{-1}. Light was provided by a 150-W quartz halogen projector bulb. Measurements were made periodically throughout the drying period between 0900 and 1600 hours; TSW in the pot was determined immediately after gas-exchange measurements.

For gas-exchange measurements in the field, leaf temperature was 24°C, PFD was 1900 µmol m^{-2}s^{-1} or greater, v was 2.3 kPa, and CO_2 concentration inside the cuvette was 335 ± 5 µL L^{-1}. Light was from sunlight or a 150-W projector lamp. Measurements were made in June and early July between 0830 and 1500 hours.

Leaf water potential (ψ) was measured with a pressure chamber (PMS Instruments Co., Corvallis, Oregon) immediately after gas-exchange measurements on the same leaf.

Calculations and Statistical Analyses

A, E, and g_w (leaf plus boundary layer) were calculated according to Caemmerer and Farquhar (1981). Ambient atmospheric pressure at the INEL is about 85 kPa (field measurements) and at Pocatello, Idaho, is about 86 kPa (greenhouse measurements). Statistical analyses were

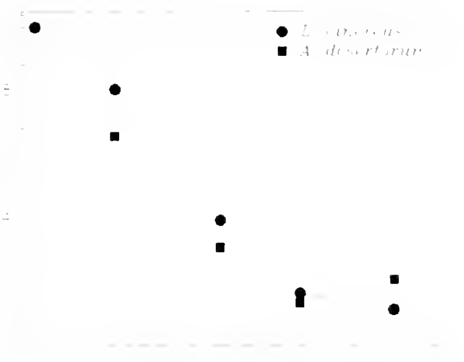

Fig. 2. Relative leaf elongation rate (LER) of the youngest leaf on vegetative tillers, expressed as a percentage of controls, vs. time after withholding water from *Agropyron desertorum* and *Leymus cinereus* plants growing in 49-L pots in a greenhouse. See Table 1 for statistical analyses.

performed with the general linear models procedure of SAS (SAS Institute 1982).

RESULTS

Following the withholding of water, TSW was consistently lower in pots containing *L. cinereus* than in those containing *A. desertorum* (Fig. 1A). The more rapid decline in TSW in *L. cinereus* pots early in the experiment may reflect the larger size of that species, but, if plant size or growth rate was responsible for observed species differences in TSW, differences would have diminished with time. That did not occur. Thus, the significant species differences and species-by-treatment interaction (Table 1a) show that water-stressed *L. cinereus* plants were capable of extracting more water from the soil than were stressed *A. desertorum*. The volumetric soil water content at the lower limit of extraction (day 50) was 13.3% and 10.3% for *A. desertorum* and *L. cinereus*, respectively.

The time courses of soil water potential, averaged over all four positions in a pot and over all pots with water-stressed plants, are shown in Figure 1B. Water potential depended on location within the pot (Table 1b), with lower water potentials occurring at higher positions in the soil profile. Soil water potentials in pots containing *L. cinereus* were significantly lower than those of *A. desertorum* after day 5 (Fig. 1B, Table 1b).

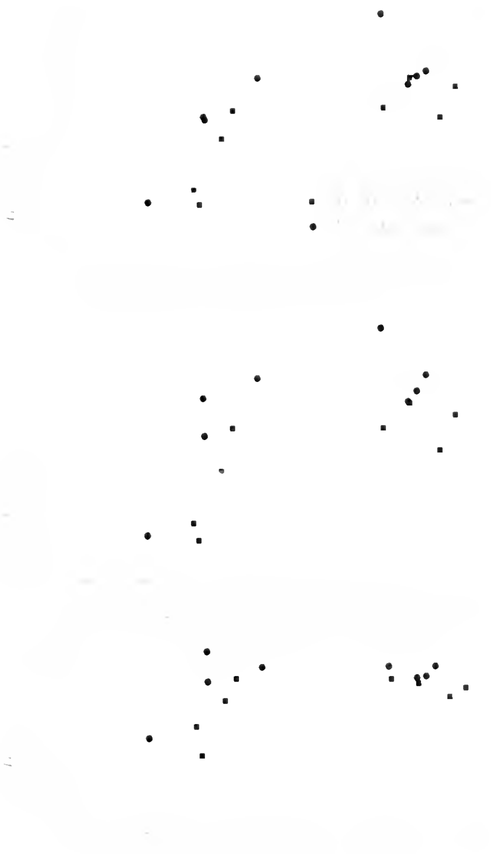

Fig. 3. Net photosynthesis (A), leaf conductance to water vapor (g), and intercellular concentration of carbon dioxide (c_i) for *Agropyron desertorum* and *Leymus cinereus* plants vs. total soil water in 49-L pots. The curves were fitted using an inverse secant transformation of soil water content; see Table 2 for equations and values of constants. Measurements were made at a leaf temperature of 25 C, a leaf-to-air vapor pressure gradient of 2.0 kPa, an ambient CO_2 concentration of 330–340 μL L^{-1}, and a photosynthetic photon flux density of 1900 μmol photons $m^{-2}\,s^{-1}$.

For well-watered plants, elongation rate of the youngest leaf on a tiller (LER) for *L. cinereus* (50.5 mm d^{-1}) was nearly twice that for *A. desertorum* (26.0 mm d^{-1}). Relative LER of both species decreased within 6 days after water was withheld from the stress-treatment plants (Fig. 2). Early in the period of soil drying, relative LER of stressed plants was lower for *A. desertorum* than for *L. cinereus*, resulting in a significant species-by-stress interaction (Table 1). This suggests that leaf elongation may be more sensitive to water stress in *A. desertorum* than in *L. cinereus*.

TABLE 2. Analyses of covariance for net photosynthesis, leaf conductance to water vapor, and intercellular CO_2 concentration (c_i) of *L. cinereus* and *A. desertorum* plants grown in 49-L pots in a glasshouse (see Fig. 3). The classification variable was species (SP: *A. desertorum*, Agde, and *L. cinereus*, Leci). The covariate (X) was a transformation of total soil water (TSW) expressed as percent of the water content at field capacity. The general form of the transformation was X = $\sec^{-1}$(TSW + C), where $\sec^{-1}$ is the inverse secant function and C is a constant, determined by iteration and given separately for both species.

				Constant		R^2	
Item	Effect Species	TSW	SP × TSW	Agde	Leci	Agde	Leci
Photosynthesis (n = 16)	*P* < .004	*P* < .0001	*P* < .004	26.0	−7.8	.86	.83
Conductance (n = 16)	*P* < .04	*P* < .0001	–	−26.5	−13.9	.83	.83
Intercellular CO_2 (n = 16)	*P* < .002	*P* < .005	*P* < .004	−27.1	−19.5	.67	.86

The relationship between A or g_w and TSW for both species is shown in Figure 3. To facilitate statistical analyses, numerous models were fitted to the data by linear regression and transformation of the dependent and/or independent variable. The model that consistently provided the best fit considering all data sets was:

$$Y = b_0 + b_1 \sec^{-1}(TSW + C)$$

where Y is net photosynthesis or leaf conductance, $\sec^{-1}$ is the inverse secant function, C is a constant, b_0 is the intercept, and b_1 is the slope. The constants were determined iteratively by substituting values for them until the highest coefficient of determination (R^2) was obtained. Values of C and R^2 are given in Table 2 for the curves shown in Figure 3.

Analyses of covariance were performed for each gas-exchange variable using species as a classification variable and the inverse secant transformation of TSW as the covariate (Table 2). *L. cinereus* had higher A and g_w than *A. desertorum* at both high and low levels of TSW (Fig. 3, Table 2). When soil water availability was expressed in relative terms, i.e., ESW, the responses of the two species were similar. Both [illegible] A and g_w until extractable water content declined to about 15%; marked reductions of A and g_w occurred at lower levels of ESW (data not shown).

Intercellular CO_2 concentrations (c_i) were higher in leaves of *L. cinereus* than in *A. desertorum* over a wide range of soil water contents (Fig. 3, Table 2). Therefore, under comparable atmospheric conditions *L. cinereus* lost more water per unit of carbon gained than did *A. desertorum*, which reflects the additional cost of water paid to achieve higher A.

A and g_w of plants sampled in the field in late spring and early summer were positively correlated with ψ measured concurrently (Fig. 4). For both species, A was more closely correlated with ψ than was g_w, and the correlation coefficients were higher for *L. cinereus* than for *A. desertorum*. At the time field sampling was initiated, *L. cinereus* plants were considerably more water stressed than were *A. desertorum* plants because of differences in ESW in the plots at the beginning of the growing season (data not shown). This difference is reflected by the highest ψ values recorded for the two species (Fig. 4). As a consequence, the highest rates of A were lower for *L. cinereus* than for *A. desertorum* and were considerably lower than the maximum A of *L. cinereus* observed in the greenhouse (Fig. 3) or for well-watered plants in the field (Anderson et al. 1993). That most *L. cinereus* plants were stressed while some *A. desertorum* were not may account for the higher correlation coefficients for *L. cinereus*. Data in Figure 4 indicate that A and g_w were generally lower in severely stressed *A. desertorum* than in *L. cinereus* at comparable ψ, which is consistent with findings from the greenhouse study.

The relationship between A and g_w is similar for the two species when grown either in the field or greenhouse (Fig. 5). This again demonstrates that the higher A in *L. cinereus* was a consequence of higher g_w rather than a higher photosynthetic capacity. Field-grown plants had

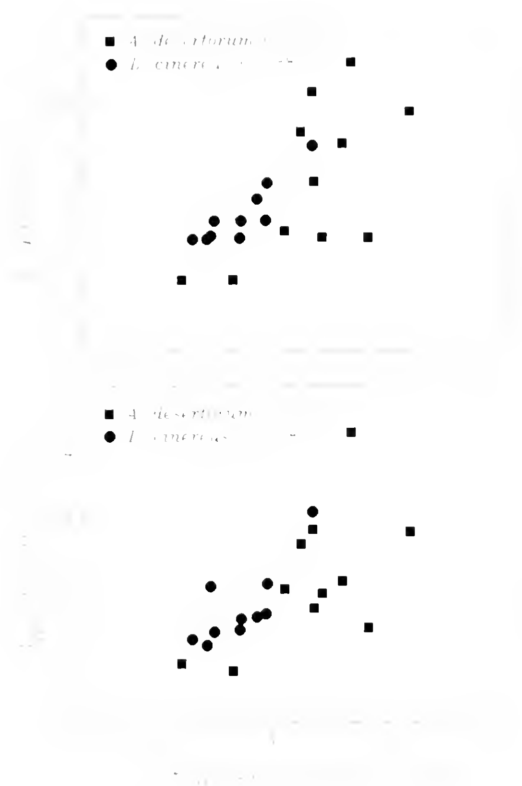

Fig. 4. Net photosynthesis (A) and leaf conductance to water vapor (g_w) for field-grown *Agropyron desertorum* and *Leymus cinereus* plants as a function of leaf water potential, measured concurrently. Gas-exchange measurements were made at leaf temperature of 24 C, a leaf-to-air vapor pressure gradient of 2.3 kPa, an ambient CO_2 concentration of 330–340 μL L^{-1}, and a photosynthetic photon flux density 1900 μmol photons $m^{-2}s^{-1}$. Trend lines were fitted by linear regression with leaf water potential taken as the independent variable (solid line = *L. cinereus*, dotted line = *A. desertorum*).

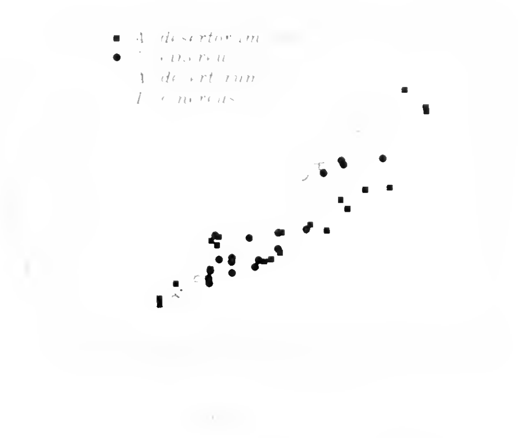

Fig. 5. Leaf conductance to water vapor (g_w) versus net photosynthetic rate (A) for *Agropyron desertorum* and *Leymus cinereus* plants grown in the field (closed symbols) or in a glasshouse (open symbols). Gas-exchange measurements were made over a wide range of soil water availabilities; cuvette conditions were the same as in Figure 4. Trend lines for glasshouse-grown plants (solid line) and field-grown plants (dotted line) were fitted by linear regression with A taken as the independent variable (Schulze and Hall 1982).

higher A for a given g_w compared to greenhouse-grown plants (Fig. 5). The intercept of the regression of g_w on A did not differ significantly from zero for field-grown plants, indicating that WUE was quite constant over the range of A and g_w measured (Schulze and Hall 1982). However, the regression line did not pass through the origin for plants grown in the greenhouse ($P <$ .05), which suggests that WUE decreased with increasing A and g_w.

DISCUSSION

Results of the greenhouse study confirmed our suspicions, based on data from monocultures grown in the field (see Anderson et al. 1987), that *L. cinereus* plants could extract more water from a soil profile than could *A. desertorum*. In addition, *L. cinereus* maintained higher A at low ψ compared to *A. desertorum*. These data suggest that *L. cinereus* might have a competitive advantage, should the two species co-occur. It is important to remember, however, that *A. desertorum* is naturalized in western North America, and so the species did not coevolve.

L. cinereus achieved higher A by maintaining a higher c_i through higher stomatal conductances. Thus, there was an additional water cost per unit carbon gained. The large stature of *L. cinereus* plants suggests a high water requirement, and indeed stands of this species can use copious amounts of water (Anderson et al. 1987). As a consequence, *L. cinereus* typically is found on deep soils or areas that receive runoff water from adjacent sites (Miller et al. 1982, Walker and Brotherson 1982, Roundy 1983). On such sites its capacity to dry a soil to lower water contents may exclude potential competitors. Indeed, it often occurs in pure or nearly pure stands on such sites. Sirotnak (1990) showed that there was intense intraspecific competition in a stand of *L. cinereus*, and the *L. cinereus* plants reduced leaf water potentials of neighboring *Chrysothamnus nauseosus* shrubs. [illegible] lower water use efficiency of *L. cinereus* is likely disadvantageous, however, on sites where total water available over the growing season is more limited. Mortality of *L. cinereus* plants was greater than that of *A. desertorum* on our experimental field plots during a severe drought in 1987–88 (unpublished observations).

In contrast to *L. cinereus*, *A. desertorum* establishes well and thrives on shallow soils and very arid sites (Rogler and Lorenz 1983). Its success on such sites probably reflects a smaller size at maturity (even under well-watered conditions), the ability to withstand prolonged drought, and prolific production of viable seeds (Hull and Klomp 1967, Marlette and Anderson 1986, Pyke 1990). Caldwell and his colleagues at Utah State University have shown that *A. desertorum* is a vigorous competitor for water and soil nutrients (reviewed by Dobrowolski et al. 1990). Its competitive ability reflects, at least in part, the production of thin roots that enable it to extract water rapidly from the soil (Eissenstat and Caldwell 1988).

It seems probable that the ability of *L. cinereus* to reduce soil water content to lower levels than those of soil supporting *A. desertorum* reflects lower osmotic potentials in leaves of *L. cinereus*. We attempted to estimate osmotic potential of greenhouse-grown plants from pressure-volume curves, but leaves of *L. cinereus* were so brittle that we were unable to obtain reliable data. Concurrent measurements of leaf relative water content (RWC) and water potential of field-grown plants showed that, for a given RWC, *L. cinereus* had lower ψ than did *A. desertorum* (data not shown; $P < .04$ by analysis of covariance). This difference between species could arise from a greater degree of osmotic adjustment (lower osmotic potential at a given RWC) by *L. cinereus* compared to *A. desertorum*.

Kuang et al. (1990) postulate that the factor that causes a reduction in LER as the soil dries is not known. Osmotic adjustment in the [illegible]. Their results show that the proportional change in LER due to osmotic adjustment was much smaller in lupin than in wheat, which suggests that LER in species with greater osmotic adjustment might be less sensitive to the [illegible] response to drying soil. Thus, the observation that LER was reduced relatively less in *L. cinereus* than in *A. desertorum* over the first 3 weeks of the drying period (Fig. 2) also may reflect greater osmotic adjustment in *L. cinereus*.

Previous studies have shown that leaf expansion frequently is more sensitive to water stress than is photosynthesis (Begg and Turner 1976). As reported here for two perennial tussock grasses, Kuang et al. (1990) found that LER in wheat and lupin was reduced almost immediately after withholding water. They demonstrated that LER decreased in response to drying soil even when leaf turgor was maintained, and they suggested that leaf growth, stomatal conductance, and osmotic adjustment are all controlled by the balance of leaf phytohormones as influenced by hormones produced in the roots. Given the frequent observation that A and g_w are closely correlated (e.g., Fig. 5), it would seem reasonable to add photosynthetic capacity to the list.

The relationship between g_w or A and TSW (Fig. 3) indicates a close coupling between leaf gas exchange and soil water content, as has been reported for a number of herbaceous and woody species growing in a variety of soils (Gollan et al. 1985, Turner et al. 1985, Sinclair and Ludlow 1986, Henson et al. 1989). Turner et al. (1985) and Gollan et al. (1985) demonstrated that although g_w and ψ often were correlated, the nature of the relationship was dependent upon environmental conditions and the rate of soil drying. Thus, they found no unique relationship between g_w and ψ and postulated that g_w and A are controlled by the level of water in the soil rather than in the leaf. Subsequent studies have confirmed that hypothesis, showing that the roots "sense" water availability or some related parameter in the soil and transmit signals to the leaves that control their behavior (Gollan et al. 1986, Masle and Passioura 1987, Passioura 1988, Henson et al. 1989, Zhang and Davies 1989, 1991, Tardieu et al. 1991). Our data are consistent with this model; for both species, g_w and A were closely related to soil water content (Fig. 3). Rather than showing a cause-and-effect relationship, the correlations between g_w and ψ (Fig. 4) likely reflect co-variation in response to declining soil moisture supplies.

In conclusion, this study shows that there may be small but significant differences in the extent to which cold-desert species can dry a soil profile. Such differences may be important in competitive interactions (Caldwell 1985). Compared with *A. desertorum*, *L. cinereus* maintains higher photosynthetic rates as soil moisture supplies decline, but it does so by maintaining a higher conductance, not through a greater photosynthetic capacity.

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ON THE RELATIVE IMPORTANCE OF FLORAL COLOR, SHAPE, AND NECTAR REWARDS IN ATTRACTING POLLINATORS TO *MIMULUS*

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ABSTRACT.—Pollinator preferences were observed for the six species of section *Erythranthe* of the genus *Mimulus* using greenhouse-grown plants placed in a meadow in the Red Butte Canyon Natural Area, Salt Lake County, Utah. The principal pollinators were hummingbirds and bumble bees. Hummingbirds preferred the species with the most reflexed tubular flowers regardless of color, whereas bumblebees preferred pink, lavender, or yellow flowers to red flowers regardless of shape. Results for the six species were confirmed by observations of F_2 hybrid recombinant plants selected such that flower color could be held constant and flower shape varied and vice versa.

Key words. Mimulus, *hummingbirds, bumblebees, flower color, flower shape, pollinators, speciation.*

The dependence of animal-pollinated plants on biotic vectors for pollen transfer has, in many cases, led to the evolution of floral adaptations that benefit one class of pollinators, for example in this study, hummingbirds or bumblebees, but discourage or exclude other potential visitors (Meeuse 1961, Procter and Yeo 1972, Faegri and van der Pijl 1979, Percival 1979, Wyatt 1983, Meeuse and Morris 1984). These adaptations include (1) floral color, which is important for long-distance recognition and attraction; (2) floral morphology, which may be an attractant as well as a determinant of the effectiveness of pollination by these visitors; and (3) floral rewards, the ultimate reason for pollinator visits.

FLORAL COLOR.—Hummingbirds are commonly said to have evolved a preference for red or orange-red flowers (K. Grant 1966, K. Grant and V. Grant 1968, Raven 1972, Faegri and van der Pijl 1979, Meeuse and Morris 1984). However, in artificial hummingbird feeding preference experiments, no color preferences were detected (Bené 1941, 1945, Wagner 1946, Collias and Collias 1968, Miller and Miller 1971, Stiles 1976, Goldsmith and Goldsmith 1979), nor were color preferences detected in most (George 1980, McDade 1983) but not all (Vickery 1992) natural experiments. In contrast, bumblebees are commonly reported to eschew red flowers (Scogin 1983), although von Frisch (Heinrich 1979) some years ago had shown bees to have a wide spectrum of color vision (Kevan 1983).

FLORAL MORPHOLOGY.—Hummingbirds are generally considered to prefer tubular-shaped flowers (K. Grant and V. Grant 1968). Yet, artificial experiments show that hummingbirds freely visit radial, relatively flat flowers (Graham Pyke personal communication). Bumblebees visit all shapes of flowers, although they appear to prefer flowers with a landing platform and/or a nectar guide (Percival 1979).

FLORAL REWARDS.—Nectar appears to be the underlying attraction to hummingbirds and nectar and/or pollen to bees (Free 1970, Heinrich and Raven 1972, Heinrich 1975, 1976, Stiles 1976, Búrquez and Corbet 1991).

Because these adaptations—floral color, floral shape, and nectar rewards—determine the identity or kind of the pollinator, changes in floral traits can potentially cause a shift in pollinators (e.g., from bees to hummingbirds), thus leading to reproductive isolation and possibly, subsequently, to speciation. This well may have happened in *Penstemon* (Straw 1956) and *Aquilegia* (Chase and Raven 1975) and may be happening in *Rhapanus sativus* color morphs (Stanton 1987) and in the monkey flower species of section *Erythranthe*.

The six species of section *Erythranthe* include a single, pink-flowered, bee-pollinated species, *M. lewisii* Pursh, and five red-flowered,

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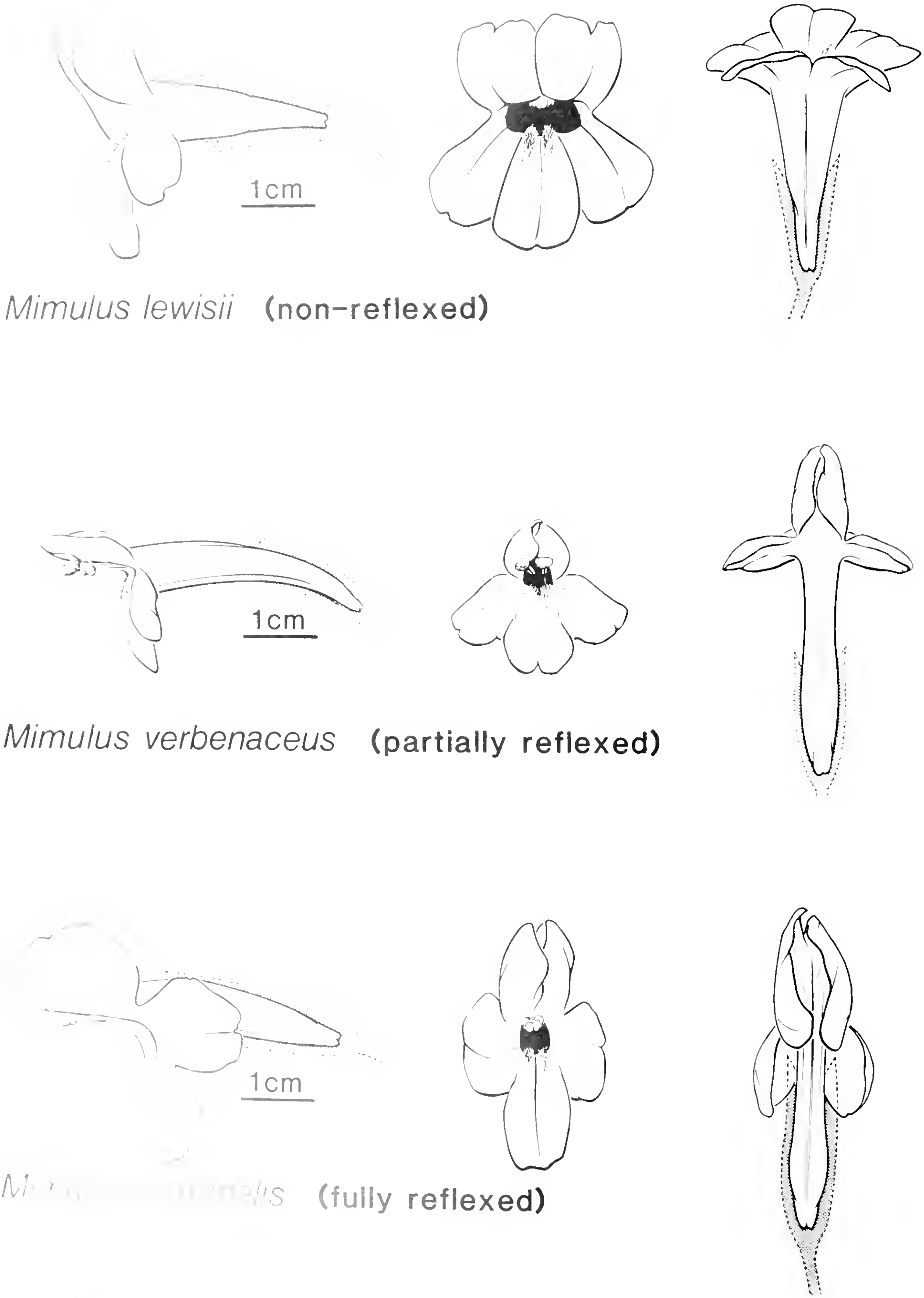

Fig. 1. [illegible] section of the genus *Mimulus*.

hummingbird-pollinated species, *M. rupestris* Greene, *M. eastwoodiae* Rydberg, *M. nelsonii* Grant, *M. cardinalis* Douglas, and *M. verbenaceus* Greene (Hiesey et al. 1971, Vickery 1978, 1987).

The bee-pollinated species, *Mimulus lewisii*, has a wide distribution from southern California northward to southern Alaska and eastward to northwestern Colorado. Flowers vary in intensity of color from light lavender-pink (Sierra Nevada race) to deep magenta-pink (Rocky Mountain race). The corollas are non-reflexed (Fig. 1, and see color illustrations in Vickery and Wullstein 1987); that is, the corolla lobes are at right angles to the axis of the corolla tube or are even thrust forward as in the Sierra Nevada race. The corolla throats have a pair of hairy ridges that serve as tongue guides for pollinators. Also, the throats display dark nectar guides under UV light.

Of the five hummingbird-pollinated species, three have restricted distributions. *Mimulus rupestris* is a narrow endemic that grows on shady cliff faces in the Sierra de Tepoztlan, ~70 km south of Mexico City, Mexico. *Mimulus rupestris* flowers vary from pinkish red to cardinal red in different populations. The flowers (Fig. 1) vary from non-reflexed, actually thrust forward in the pinkish red–flowered population (9102), to partially reflexed in other populations. In partially reflexed flowers the upper pair of corolla lobes is strongly reflexed, but the lateral pair and the labellum are not. *Mimulus eastwoodiae* is endemic to moist areas, "hanging gardens" in protected overhangs in sandstone shelter caves in southeastern Utah and northeastern Arizona. It has cardinal red, partially reflexed flowers. *Mimulus nelsonii* is a broad endemic found along streams in limited areas high in the Sierra Madre Occidental in the states of Durango and Sinaloa, Mexico. It, too, has cardinal red, partially reflexed flowers. The other two hummingbird-pollinated species of section *Erythranthe* have wider distributions. *Mimulus verbenaceus* is distributed in northern Mexico (Sonora) through Arizona into southern Utah. *Mimulus verbenaceus* flowers are cardinal red and partially reflexed. *Mimulus cardinalis* is distributed along the Pacific coast from central Baja California to southern Oregon and inland into Nevada and Arizona. *Mimulus cardinalis* flowers vary from yellow to orange to orange red to cardinal red, in different populations. A few populations are mixed, e.g., yellow and red. *Mimulus cardinalis* flowers are fully reflexed; that is, the upper and lateral corolla lobes are sharply turned back and the labellum is folded back on itself (Fig. 1). The more reflexed the flowers are, the more tubular they appear. The corollas of all red-flowered species have tongue guides like the pink-flowered species but lack nectar guides under UV light.

All six species produce bisexual, that is, perfect, flowers and are self-compatible. The flowers of all five red-flowered species contain the same set of six anthocyanin pigments—cyanidin-3-glucoside, cyanidin-3-rhamnoglucoside, cyanidin-3-caffeoyl glucoside, pelargonidin-3-glucoside, pelargonidin-3-rhamnoglucoside, and pelargonidin-3-caffeoyl glucoside—and the same carotene pigment (Pollock et al. 1967). The flowers of pink-flowered *M. lewisii* have the same three cyanidin pigments, but they lack the three pelargonidins and the carotene pigment is restricted to red dots in the corolla throat. Variations in flower color of the different species, populations, and hybrids reflect variations in the presence, amounts, and floral locations of the anthocyanin and carotene pigments. In addition, we have identified three different pairs of genes in *M. cardinalis*, *M. verbenaceus*, and *M. lewisii* that turn off anthocyanin production when homozygous recessive, leading to yellow flowers due to the remaining carotene pigment in *M. cardinalis* and *M. verbenaceus* and to white flowers in *M. lewisii*, which lacks carotene. For further information on the morphology, distribution, physiology, genetics, and taxonomy of the group see A. Grant (1924), Pennell (1951), Hiesey et al. (1971), and Vickery (1978, 1987).

The six species of section *Erythranthe* form a promising group for investigating the basic question of this study: What floral traits are responsible for attracting particular pollinators, specifically, hummingbirds and bumblebees, to flowers?

MATERIALS AND METHODS

Experimental Design

The experimental design for this study of pollinator attraction for the species and hybrids of section *Erythranthe* has two parts. First, in experiment 1 we plan to observe the pollinator preferences for the six species comprising the section in relation to their flower colors, flower shapes, and nectar rewards. Second, in experi-

[illegible] The species and hybrids of section *Erythranthe* used in the experimental field

M. cardinalis **Douglas**
[illegible] yellow color morph, growing in a wash with palms and running water, elev. ca. 150 m, on north side of [illegible] Baja California Norte, Mexico (used for experimental hybridization only)
[illegible] red color morph from the same population

M. verbenaceus **Greene**
[illegible] Bright Angel Creek, near Phantom Ranch, elev. ca. 612 m, Grand Canyon National Park, Coccino
Co., Arizona

M. nelsonii **Grant**
[illegible] growing in a small brook in a pine forest, elev. ca. 2555 m, near the Sierra Madre divide on Rt. 40, Sinaloa, Mexico

M. eastwoodiae **Rydberg**
[illegible] growing in seeps in caves on high sandstone cliffs, elev. 1415 m, Bluff, San Juan Co., Utah

M. rupestris **Greene**
[illegible] growing on a conglomerate rock cliff on Tepozteco Trail, elev. ca. 2300 m, Sierra de Tepoztlan, Morelos, Mexico

M. lewisii **Pursh**
5875 growing by a small stream on Albion Basin road elev. 2680 m, Alta, Salt Lake Co., Utah
6103 growing by a small sandy stream leaving Ice Lake, Sierra Nevada, elev. ca. 2000 m, Placer Co., California (used for the experimental hybridization only)

F_1 hybrid
13258 *M. cardinalis* (13106, Cedros Island, yellow morph, corolla lobes fully reflexed)

M. lewisii (6103, Ice Lake, Sierra Nevada, lavender, corolla lobes thrust forward)

F_2 hybrid population
13600 F_1 hybrid (13258) × self

ment 2 we plan to distinguish the relative effects of color, shape, and nectar rewards. This will be done by testing plants of an F_2 hybrid population that recombine these traits such that we can (1) hold shape constant and observe the effect of different colors, (2) hold color constant and observe the effect of different shapes, and then (3) relate these results to the nectar characteristics of the plants.

Plants

Populations representative of each species (Table 1) were selected in the University of Utah greenhouse. These populations included the two color morphs, red and yellow, of *M. cardinalis* and the two races of *M. lewisii*, the Sierra Nevada lavender-pink race and the Rocky Mountain deep magenta pink race. The various [illegible] were grown from seeds collected [illegible] from populations of [illegible] of the different [illegible]

[illegible] conditions were grown [illegible] between the [illegible] of section *Erythranthe* [illegible] the yellow color [illegible] (13106) with [illegible] light lavender-pink race of *M. lewisii* with thrust forward corolla lobes (6103). The F_1 hybrid had medium pink flowers with partially reflexed upper corolla lobes. The F_1 hybrid was self-pollinated, and from it a large F_2 hybrid population of close to 1000 plants was grown. The F_2 hybrid plants recombined the parental flower shapes and nectar characteristics, and exhibited a wide array of transgressive variation in flower color—red, yellow, light lavender-pink, light pink, medium pink, and deep magenta-pink. As would be anticipated from the genetic control of anthocyanin production (see above), there were relatively few red-flowered F_2 hybrid plants. Also, there were very few with corolla lobes thrust forward.

METHODS

Experiment 1
Floral Visitor Preferences for the Species

To determine floral preferences of the potential pollinators for the six species of section *Erythranthe*, plants of each species (except *M. nelsonii*) plus the F_1 hybrid of *M. cardinalis* × *M. lewisii* were placed for observation in a moist meadow in Red Butte Canyon Natural Area in the Wasatch Mountains (elevation 1980 m, Salt Lake City, Utah).

Due to problems in initiating flowering in *Mimulus nelsonii* in 1985, this species was not available for study until the next year. Fortuitously, the 1986 results for *M. nelsonii* could be included in the analysis because the findings for the three other red-flowered species common to both experiments (de facto controls) were insignificantly different from 1985 to 1986 even though year-to-year changes in climate and pollinator guilds usually might lead to significant differences.

Nine potted plants of each species and of the F_1 hybrid were placed on top of inverted, one-gallon, black plastic pots to raise the flowers above the surrounding meadow vegetation and increase their visibility to potential floral visitors. Pots were placed at 1-m intervals in a 5 × 9-m grid. Within the first row, the five species and F_1 hybrids were randomly positioned. This relative sequence was maintained in the subsequent rows, but the position was shifted three places in adjacent rows. This arrangement resulted in each species being surrounded by the other four species or the F_1 hybrid.

The populations were observed for 2–3 hours at different times of day from early dawn to dusk for seven days in late June and early July for a total of 20 hours. The weather was consistently clear, warm, and sunny. Numbers and identities of potential pollinators making close approaches to the flowers and numbers of open flowers for each species and the F_1 hybrid were recorded daily. An approach, for this study of floral traits that attract pollinators, was considered to be a close approach to a flower generally followed by an actual visit, that is, by a hummingbird thrusting its beak into the flower or a bumblebee landing on and entering the flower. At the end of the experiment, day 8, flowers were destructively sampled at dawn (before pollinator visitation) to determine the amount and quality of available nectar. The data were examined, using chi square and Spearman rank correlation methods (Sokal and Rohlf 1969), for patterns of floral visitor preference in floral color, shape, and/or nectar rewards.

Experiment 2
Pollinator Preferences for Flower Color/Shape

To discriminate between the relative attractiveness of flower shape and flower color, it was necessary to have a population of plants with all three major flower shapes—non-reflexed, partially reflexed, and fully reflexed—in each of the several colors. Such a set was obtained by self-pollinating the F_1 hybrid of *M. cardinalis* (13106) × *M. lewisii* (6103) (see Table 1). We selected a subset of plants from the resulting F_2 recombinants with fully reflexed, partially reflexed, and non-reflexed flowers in red, yellow, and four tints and shades of pink. Too few "thrust forward"-flowered F_2 plants were obtained to analyze the fourth shape category in this experiment. Insufficient red-flowered F_2 hybrids were obtained, and so three native but corresponding red-flowered species—non-reflexed *M. rupestris*, partially reflexed *M. verbenaceus*, and fully reflexed *M. cardinalis*—were substituted. *Mimulus nelsonii* was added to the experiment to fill the data gap in the previous year's experiment. The F_2 hybrids also recombined the nectar characteristics of volume, concentration, and sugar content, but these were not selected. Thus, the second experiment included, in addition to *M. nelsonii*, plants of the three major shape classes in each of six color categories combined with various, but unselected, nectar traits.

Plants of the F_2 hybrid population, including the red-flowered species to be tested, were raised in the greenhouse in spring 1986. Five plants of *M. nelsonii* and five of each color-shape category were placed in the study area in Red Butte Canyon in late June. The pots were randomly arranged at 1-m intervals on inverted pots in an 11 × 9-m grid. Close approaches by major pollinators (hummingbirds and bumblebees) were recorded daily for six days. Approaches or actual visits by other pollinators, e.g., flies, were rare. For each major type of potential pollinator, the total number of approaches for a given day was divided by the number of open flowers to determine a daily average close approach rate for each color-shape category. This value was standardized by dividing by the overall mean approach rate for that day to compensate for daily variations in number of pollinator approaches and/or length of observation periods (Sutherland and Vickery 1988). The daily standardized rates were then averaged to produce mean pollinator approach rates for each color-shape category. To test whether significant differences in pollinator approach rates to each color-shape category occurred, a two-way analysis of variance was performed (Sokal and Rohlf 1969). If significant differences were detected, Student Newman-Keuls test was then conducted to ascertain where the significant differences occurred (Sokal and Rohlf 1969). To test for significant temporal differences in pollinator approach rates, a Kendall coefficient of concordance test was performed (Gibbons 1976). To test whether hummingbirds were learning during the experiment to associate flower shape and/or flower color with nectar rewards, daily approach rates to the 18 color-shape categories, 6 color classes, and 3 shape categories were ranked (low to high) and compared using the Kendall coefficient of concordance. To test the hypothesis that bumblebees were learning during the experiment (i.e., that they were altering their foraging preferences with time and experience), daily visitation rates to the 18 color-shape categories, 6 color classes, and 3 shape categories were ranked (low to high) and compared using the Kendall coefficient of concordance.

Nectar characteristics were ascertained at the termination of each experiment, day 8 for experiment 1 and day 7 for experiment 2. Flowers were destructively sampled and nectar volumes and concentrations measured. Nectar volume was measured with a calibrated 5 µl micropipette. Nectar concentration, for the same set of samples, was measured as sucrose equivalents (weight per total weight basis) with a pocket refractometer. Average sugar production was calculated by converting nectar concentration (sucrose equivalents) to weight per volume (using values given in the CRC Handbook of Chemistry and Physics [1978]) and multiplying this value by nectar volume (see Bolten et al. 1979 for details). To test whether significant interspecific (experiment 1) or color-shape category (experiment 2) differences existed in nectar volume, nectar concentration, and/or [illegible] series of single classification [illegible] (Sokal and Rohlf 1969) [illegible] significant interspecific differences [illegible] Student Newman-Keuls [illegible] was then conducted [illegible] which species or [illegible] and/or shape [illegible] differences occurred. [illegible] compared with nectar volume [illegible] and sugar production [illegible] correlation [illegible]

RESULTS AND DISCUSSION

Floral Visitors

Floral visitors observed in both experiments were principally hummingbirds and bumblebees, with only negligible visits by flies. They were active all day. The majority of hummingbird visits were by Broad-tailed Hummingbirds (*Selasphorus platycercus*), a highly migratory species found throughout the range of the species of section *Erythranthe*. In addition, visits by Calliope (*Stellula calliope*), Black-chinned (*Archilochus alexandri*), and perhaps other species of hummingbirds were observed. In other areas of the range other species would surely be observed as well (Johnsgard 1983). The majority of observed bee visits were made by *Bombus appositus* and *B. huntii*, although *B. bifarius*, *B. centralis*, *Psithyrus insularis*, and *P. suckleyi* were observed also.

Experiment 1
Pollinator Preferences for the Six Species

Results (Table 2) of the overview of the six *Erythranthe* species indicate that hummingbirds did not approach flowers of the various species in proportion to their frequency in the experimental population ($\chi^2 = 228.8$, $P < .001$). Hummingbirds significantly preferred cardinal red, fully reflexed *M. cardinalis* flowers; they neither preferred nor avoided partially reflexed, cardinal red species, but significantly avoided pinkish-red, non-reflexed *M. rupestris* and pink, non-reflexed *M. lewisii* flowers (Table 2). These results could be interpreted as showing an avoidance of non-pure red. However, amongst the cardinal red–flowered species the strong preference for strongly reflexed *M. cardinalis* compared to the equally red but partially reflexed species suggests to us that hummingbirds may be showing a preference for red, but probably also an attraction to flower shape. Indeed, ranking the species by increasing degree of reflexion, *M. rupestris* < *M. lewisii* < *M. verbenaceus* = *M. nelsonii* = *M. eastwoodiae* < *M. cardinalis*, nicely corresponds to the ranking of the species by increasing hummingbird approaches (Table 2). Floral shape appears to be the main proximate cue for hummingbird approaches under these conditions.

Bumblebees also were not attracted to all the species in proportion to their frequency in the experimental population ($\chi^2 = 297.1$, $P < .001$). While individual bees would show particular

TABLE 2. Results of experiment 1. Flower number, pollinator approaches, and quantity and quality of nectar rewards for the 6 species of section *Erythranthe* and the F_1 hybrid of *M. cardinalis* × *M. lewisii*. Means of 7 days of observations. Within a column, approach rates with the same subscript do not differ significantly ($P > .05$).

	Hummingbird visits			Bumblebee visits			Nectar		
	Number of flowers	Number of approaches	Approaches per 100 flowers	Number of flowers	Number of approaches	Approaches per 100 flowers	Concentration (%)	Volume (µl)	Amount of sugar (µg)
cardinalis (13249)	260	442	170_a	44	0	0_a	13.4	4.9	71.1
verbenaceus (5924)	533	604	113_b	95	1	1_a	12.8	2.6	36.1
nelsonii[1] (6271)	351	379	108_b	59	1	2_a	11.9	2.8	34.6
eastwoodiae (6079)	170	193	114_b	23	1	4_a	11.0	3.1	33.0
rupestris (9102)	95	27	28_c	7	0	0_a	10.4	2.1	22.8
lewisii (5875)	156	53	34_c	155	208	134_b	15.6	1.3	12.6
F_1 hybrid (13,258)	51	60	118_b	42	56	133_b	13.6	4.1	56.5

[1] Results from 1986 season. Controls showed them to be comparable.

preferences (Heinrich 1979), overall, the bees significantly preferred pink-flowered, non-reflexed *M. lewisii* to the red-flowered species (Table 2), whether non-reflexed, partially reflexed, or fully reflexed. Thus, these results suggest to us that bumblebees are attracted primarily by flower color and not shape under these conditions.

The ultimate reason for pollinator visits to the flowers is to collect floral rewards, i.e., nectar and/or pollen. In monkey flowers the nectaries are hidden from view; therefore pollinators cannot ascertain the quantity or quality of nectar rewards from a distance (Meeuse and Morris 1984). So, apparently, pollinators have to associate visible floral clues such as shape or color with nectar rewards (Waser 1983).

When hummingbird approach rates to the six species are compared with average nectar volume and average sugar production of those species, there are significant correlations (r_s = .96, $P = .001$, r_s = .93, $P < .01$, respectively). There is no correlation with average nectar concentration (r_s = .57, $P > .10$) using Spearman rank correlations in each case. Hummingbirds seem to be making foraging decisions on the basis of either nectar volume or sugar production rather than nectar concentration. Inasmuch as most of the species are red-flowered, hummingbirds appear to be relying on floral shape cues (specifically petal reflexion) as an indicator of the hidden nectar rewards of the various species.

When bee approach rates to the six species are compared with average nectar concentration, average nectar volume, and average sugar production, there are no significant correlations (r_s = .46, $P > .10$; r_s = .35, $P > .20$; and r_s = −.38, $P > .20$, respectively) using Spearman rank correlations. Perhaps this is because bumblebees often collect pollen as well as, or instead of, nectar (Heinrich 1979). Therefore, their foraging process is more complex than that of hummingbirds, which forage for nectar only.

Medium pink, partially reflexed F_1 hybrid flowers attracted both hummingbirds and bumblebees (Table 2). F_1 hybrids showed a lower hummingbird visitation rate than their *M. cardinalis* parent but a much higher rate than their *M. lewisii* parent. The hummingbird visitation rate to F_1 hybrids was insignificantly different from the rates to the partially reflexed species. F_1 hybrids have the same bumblebee visitation rate as *M. lewisii*. The partially reflexed flower shape of the F_1 hybrids would seem to be attracting hummingbirds, whereas their medium pink flower color would seem to be attracting bees.

TABLE 3. [illegible] Mean standardized hummingbird approaches per flower for six color and three shape [illegible] with the same subscripts do not differ significantly ($P > .05$).

[illegible]	Flower shape			
	Non-reflexed	Partly reflexed	Fully reflexed	Mean
Red	0.482	1.056	1.347	0.862_a
Yellow	0.730	0.990	1.213	0.978_a
Lavender-pink	0.584	1.047	1.108	0.913_a
Light pink	0.658	1.000	1.414	1.024_a
Medium pink	0.652	1.126	1.145	0.974_a
Magenta pink	1.086	1.073	1.190	1.116_a
[illegible]	0.649_a	1.049_b	1.236_c	

Experiment 2
Pollinator Preferences for Flower Color/Shape

HUMMINGBIRDS.—Results (Table 3) of the analysis of approach rates in relation to floral color and floral shape by means of a 2-way ANOVA indicate that hummingbirds (1) did not discriminate between flowers according to color ($F = 0.96$, $P > .25$) but (2) selectively visited flowers according to shape ($F = 22.11$, $P < .001$). Hummingbirds preferred fully reflexed flowers to partially reflexed flowers and partially reflexed flowers to non-reflexed flowers as adumbrated by the comparison of species results above. With the minor exception of dark pink, partially reflexed and non-reflexed flowers (where visitation rates were reversed), this preference was consistent for all color classes and shape categories.

The nectar characteristics of each shape category of F_2 hybrid plants (Table 4) were not random recombinations as might have been expected but showed a significant correlation ($\chi^2 = 3.6120$, $P < .05$) between increasing degree of corolla lobe reflexion and increasing sugar content of nectar. There appears to be genetic [illegible] between floral shape and nectar reward [illegible]. Hummingbirds seem to be [illegible] of this linkage to maximize [illegible].

Hummingbirds appear to be learning to as[illegible] with flower shape. Re[illegible] temporal association [illegible] for the 18 color-[illegible] ($W = 0.[illegible]$, $P < .01$) and the 3 shape [illegible] ($P < .05$) but no temporal [illegible] hummingbird floral preference for [illegible] ($W = 0.15$, P [illegible] .50). If fully re[illegible] [illegible] preferred, then their shape categories should have the highest ranking. If hummingbirds are perfect at distinguishing fully reflexed flowers, then the six colors of fully reflexed flowers should have rankings 13, 14, 15, 16, 17, and 18, and the sum of the rankings would be 93. An examination of the sum of the rankings for fully reflexed flowers indicates a significant increase from 69 at day 1 to 91 at day 5 (Spearman rank correlation coefficient $r_s = .90$, $P < .05$). Apparently, the birds are learning relatively quickly to select more reflexed flowers with their higher nectar volumes and sugar contents.

BUMBLEBEES.—If color is the primary factor attracting bumblebee floral visitors as experiment 1 suggests to us, and bees prefer non-red flowers, then bees should avoid the red-flowered species, *M. rupestris*, *M. verbenaceus*, and *M. cardinalis* (used in this experimental population as surrogates for the under-represented red F_2 plants), and preferentially visit the yellow and pink-flowered F_2 hybrid plants. Results for the 18 color-shape categories of experiment 2 (Table 5) indicate that bees selectively visit flowers according to color ($F = 5.06$, $P < .001$) but do not discriminate between flowers according to shape ($F = 1.03$, $P > .25$). Although bees discriminated against red flowers, there were no significant differences between visitation rates to non-red (yellow, lavender-pink, light pink, medium pink, and magenta-pink) flowers.

Results indicate a significant temporal association in bee foraging preference for the 18 color-shape categories ($W = 0.40$, $P < .01$) and the 6 color classes ($W = 0.53$, $P < .05$), but no temporal association in bee floral preference for the 3 shape categories ($W = 0.28$, $P > .20$). This

TABLE 4. Mean nectar concentration, nectar volume, and nectar sugar production for plants in the F_2 hybrid experiment.

Corolla shape Flower color	Number of flowers	Nectar concentration % ± SD	Nectar volume µl ± SD	Sugar content µgm ± SD
Non-reflexed corolla lobes				
Red	15	10.4 ± 4.2	2.1 ± 2.0	22.8 ± 24.3
Yellow	45	12.7 ± 6.7	1.2 ± 1.3	17.9 ± 22.0
Lavender-pink	50	14.8 ± 8.7	1.0 ± 1.5	16.5 ± 27.1
Light pink	50	17.2 ± 6.0	1.5 ± 1.3	26.5 ± 24.9
Medium pink	37	11.2 ± 5.8	1.4 ± 3.6	19.9 ± 64.6
Magenta-pink	40	10.7 ± 6.0	1.0 ± 1.3	12.7 ± 21.7
$\bar{x}$	39.5	12.8	1.4	19.4
Partially reflexed corolla lobes				
Red	48	12.8 ± 4.9	2.6 ± 3.2	36.1 ± 44.4
Yellow	45	11.1 ± 6.1	2.3 ± 3.2	36.4 ± 67.7
Lavender-pink	50	17.9 ± 9.0	1.0 ± 0.9	22.7 ± 28.4
Light pink	50	12.8 ± 4.8	2.0 ± 1.8	28.2 ± 29.2
Medium pink	61	12.3 ± 4.6	1.9 ± 2.3	27.5 ± 32.8
Magenta-pink	50	10.7 ± 3.4	1.2 ± 1.2	14.7 ± 19.1
$\bar{x}$	50.6	12.9	1.8	27.6
Fully reflexed corolla lobes				
Red	41	13.4 ± 3.1	4.9 ± 4.0	71.1 ± 62.1
Yellow	51	11.9 ± 4.5	3.3 ± 4.0	47.7 ± 62.3
Lavender-pink	29	12.4 ± 4.8	1.3 ± 1.8	19.5 ± 60.3
Light pink	50	12.4 ± 4.2	2.1 ± 1.7	28.6 ± 26.1
Medium pink	48	10.5 ± 5.3	0.9 ± 0.9	12.0 ± 17.9
Magenta-pink	50	12.6 ± 4.6	1.4 ± 1.6	20.7 ± 28.9
$\bar{x}$	44.8	12.2	2.3	33.3

TABLE 5. Mean standardized bee approaches per flower for six color and three shape categories. Within a row or column, means with the same subscripts do not differ significantly ($P > .05$).

	Reflexion			
Color	Non	Part	Full	Mean
Red	0.0	0.065	0.480	0.182_a
Yellow	1.312	0.798	1.046	1.052_b
Lavender	1.043	0.905	0.666	0.871_b
Light pink	1.252	1.644	1.578	1.491_b
Medium pink	1.403	0.613	1.078	1.031_b
Dark pink	1.345	0.779	1.232	1.119_b
$\bar{x}$	1.059_a	0.801_a	1.013_a	

2-way ANOVA
color F = 5.06, $P < .001$
shape F = 1.030, $P > .25$
interaction F = 0.63, $P > .75$

implies that the bees were learning and that their floral preferences for color-shape categories and color classes did, in fact, increase during the experiment.

When bee approach rates were compared to nectar characteristics (Table 3), there were no significant correlations between bee approaches and nectar concentration ($r_s = .08$, $P > .10$), nectar volume ($r_s = .29$, $P > .10$), or sugar production ($r_s = -.23$, $P > .10$).

Thus, under the conditions of Red Butte Canyon in 1985–86—the guild of pollinators [illegible] flowers [illegible] pollination [illegible] hummingbirds showed [illegible] yellow, lavender-pink, light pink, medium pink, or magenta-pink but foraged according to floral shape. They preferred fully reflexed to partially reflexed to non-reflexed flowers. On the other hand, bumblebees showed no floral shape preferences but foraged according to floral color. They avoided red flowers but visited yellow, lavender-pink, light pink, medium pink, and magenta-pink equally.

ACKNOWLEDGMENTS

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RESPONSE OF A SONORAN RIPARIAN FOREST TO A 10-YEAR RETURN FLOOD

J. C. Stromberg[1], B. D. Richter[2], D. T. Patten[1], and L. G. Wolden[1]

[illegible] March 1991, a 10-year return flood (368 m³ s⁻¹) occurred in the Hassayampa River, a perennial stream in the [illegible] Sonoran Desert. Depth of the floodwater ranged from 2.64 ± 0.20 m (mean ± SD) near [illegible] highest floodplain zone (Prosopis forest). Flow velocity was 1.7 ± 0.6 m s⁻¹ and 0.9 ± [illegible] sediment was deposited on the floodplain, with maximum deposition [illegible] 1–2 m above the water table. Native riparian vegetation showed resistance and [illegible] Plants on high floodplains (e.g., *Prosopis velutina* trees and saplings, and *Populus* [illegible] mortality. *Populus fremontii* and *S. gooddingii* "pole" trees and saplings were [illegible] varying mortality depending on floodplain elevation and depth of flood waters. [illegible] on high floodplains averaged 6% mortality, compared to 40% for those on low [illegible] where standing water was >2 m. Seedlings of *Populus fremontii* and *Salix* [illegible] abundantly after the flood along overflow channels and main channel sediment bars, contributing [illegible] these episodically recruiting species. The exotic species *Tamarix pentandra* had greater mortality [illegible] low post-flood recruitment compared to *P. fremontii* and *S. gooddingii*. Survivorship of shrub species [illegible] floodplain elevation. *Zizyphus obtusifolia* grew on high-elevation floodplains and had no mortality. [illegible] floodplains underwent mortality but revegetated after the flood via asexual reproduction. [illegible] the dominant shrub *Baccharis salicifolia* declined by half but recovered to pre-flood levels [illegible] sprouting. Dominant herbaceous plants on stream banks and low floodplains (i.e., the [illegible] grasses *Paspalum distichum* and *Cynodon dactylon*) similarly compensated for a 50% decline in [illegible] cover. The post-flood herbaceous understory vegetation in high-elevation floodplain zones (i.e., [illegible]) remained sparse throughout the summer and shifted in composition from nearly monotypic stands [illegible] mixtures of native and exotic annual grasses and forbs.

Key words: [illegible] *disturbance*, Populus fremontii, Salix gooddingii, *floodplain aggradation*.

Flood flows have been said to be the "principal driving force responsible for the existence, productivity, and interactions of the major biota in river floodplain systems" (Junk et al. 1989). With respect to floodplain vegetation, flood [illegible] integral role in the dynamics of [illegible] plant establishment, and species [illegible] maintenance of species [illegible] and nutrient cycling and [illegible] 1974, Johnson et al. 1976, [illegible] 82, [illegible] bacher 1984, [illegible] 1988, [illegible] 1989, Skog- [illegible] Riparian [illegible] peri- [illegible] generation, [illegible] 1990).

Decreased flooding is often a greater perturbation to riparian floodplains than is flooding (Sparks et al. 1990), as indicated by the substantial vegetational changes that occur when rivers are dammed and flooding is suppressed (Reily and Johnson 1982, Fenner et al. 1985, Rood and Mahoney 1990). Dam construction may result in increased riparian acreage in sediment deltas at upstream ends of reservoirs (DeBano and Schmidt 1990), but altered flow and sedimentation patterns downstream can result in decreases in plant establishment rates and loss of riparian forests (Rood and Mahoney 1990, Howe and Knopf 1991).

The size differential between base flows and flood flows of a given recurrence interval is greater in arid regions than in humid regions

(Graf 1988). Large desert floods can cause substrate erosion and plant removal in systems in which stabilizing vegetative cover has been reduced by cattle grazing, base-flow reduction, or other factors (Platts et al. 1985, Gordon-Ish-Shalom and Gutterman 1989, Stromberg and Patten 1992). This occurred in large scale in late nineteenth-century Arizona when large floods on denuded floodplains and watersheds contributed to regional erosion and downcutting of streams (Cooke and Reeves 1976). Floods also can cause local extirpation of aquatic species in areas where habitat fragmentation has reduced their ability to recolonize disturbed areas (Collins et al. 1981). In general, however, because desert stream ecosystems evolved with flooding, they are able to resist or rapidly recover after flood events (Fisher and Minckley 1978, Fisher et al. 1982, Reichenbacher 1984).

Few desert streams in the Southwest have not been modified to some degree by human activities. The opportunity arises infrequently to study large floods in relatively unimpacted systems. In February and early March 1991, rainstorms caused extensive flooding in Arizona. Three-day rainfall totals within the watershed of the Hassayampa River were 7.1 cm (Wickenburg station) to 10.1 cm (Prescott station), comprising about 25% of the annual average rainfall. This resulted in peak stream flows of 368 $m^3 s^{-1}$ (>3000 times base flow level) at The Nature Conservancy's Hassayampa River Preserve, a relatively unmodified riparian system for which there are pre-flood baseline data (Stromberg et al. 1991). A continuing series of storms and spring snowmelt produced several smaller flood peaks through the middle of April. This event provided the opportunity to study the response of the riparian ecosystem to a 10-year return flood. Our primary objectives were to quantify (1) changes in floodplain topography resulting from sediment deposition and scour; (2) survivorship of dominant riparian trees (*Populus fremontii*, *Salix gooddingii*, *Prosopis velutina*, and the exotic *Tamarix pentandra*) and shrubs (*Baccharis salicifolia*, *Hymenoclea monogyra*, *Tessaria sericea*, and *Zizyphus obtusifolia*); (3) post-flood seedling recruitment and vegetative reproduction of trees and shrubs; and (4) changes in cover and composition of herbaceous species. Secondary objectives were to compare the effects of the 10-year return flood to those of smaller prior-year floods, including a 5-year return flood (193 $m^3 s^{-1}$) in August 1988 and and a 2-year return flood (68 $m^3 s^{-1}$) in July 1990.

STUDY AREA

The Hassayampa River lies within the Gila watershed of central Arizona's Basin and Range Province and drains portions of the Bradshaw, Date Creek, and Weaver mountains. It arises at about 2350 m and flows freely and intermittently through bedrock canyons interspersed with deep alluvial basins to its confluence with the Gila River at about 240 m. South of Wickenburg in northwest Maricopa County, Arizona, a shallow bedrock layer causes perennial surface flow for about 8 km. The bedrock-confined perennial reach is supplied with alluvial and basin-fill groundwater stored in a deep basin located around Wickenburg (Jenkins 1989a, 1989b). The watershed above this point is about 1800 km^2, approximately one-third of which is composed of mountains vegetated by *Pinus ponderosa* forests. The remainder is rolling hills and valleys vegetated by Interior chaparral and Sonoran desertscrub species.

The study was conducted along a gaining section of the perennial river reach (base flows increase from 0 to 0.11 $m^3 s^{-1}$) at an elevation of 600 m within The Nature Conservancy's Hassayampa River Preserve (Jenkins 1989a). The river has a gradient of 6 m km^{-1}. The primary channel has sandy bed sediments, a width of 1–3 m, and depth of about 0.3 m. The floodplain, which ranges from about 150 to 200 m in width, in this paper is defined geomorphologically as that surface adjacent to the channel and built of materials deposited in the present regime of the river (Graf 1988). This encompasses surfaces vegetated by *Prosopis velutina* that are up to 3 m above the water table (Fig. 1), based on evidence that substrate in such areas was flood deposited (Burkham 1972, Minckley and Clark 1984). The adjacent uplands slope down to the floodplain with varying gradients. The climate is arid, with average annual rainfall of 29 cm at the Wickenburg station.

The Hassayampa River Preserve was historically grazed and used recreationally, but both impacts were eliminated in 1987 when the area was acquired by The Nature Conservancy (Richter 1992). The system may still be recovering from these prior impacts; however, there are no streams in the area that have been ungrazed for long time periods with which the

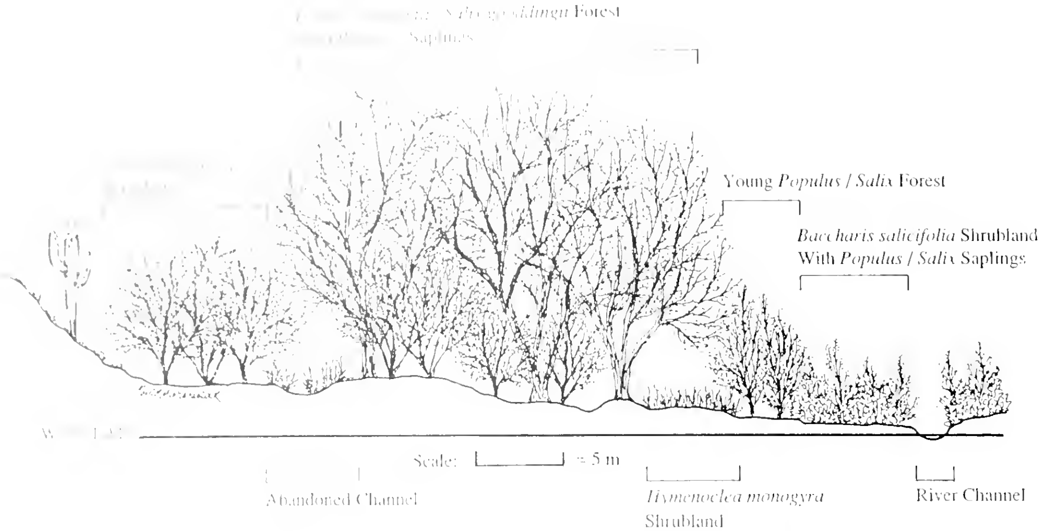

FIG. 1. Representative cross section of a portion of the Hassayampa River floodplain. Tree heights and depth to the water table not to scale.

Hassayampa River ecosystem could be compared. The herbaceous understory contains many exotic plant species, but the overstory species are predominantly native (e.g., *P. velutina*, *P. fremontii*, and *S. gooddingii*) except for a small component of *T. pentandra*. Portions of the watershed are grazed by cattle and urbanized, processes that may result in increased sediment yield or increased peak flow velocities (Von Guerard 1989, Kondolf and Keller 1991, Leopold 1991).

METHODS

Data were collected on stream discharge, floodplain aggradation and degradation, woody plant survivorship and recruitment, and herbaceous plant cover, species richness, and Shannon-Wiener species diversity. These data were obtained from the 1991 flood year and during three prior years with smaller floods. Plant nomenclature follows Lehr (1978).

Flow Data and Floodplain Sedimentation

Daily discharge (flow rate) [illegible] during the 1991 flood was measured [illegible] a stream gauge [illegible] of the per- [illegible]. Depth of sediment de- [illegible] the 1991 flood was [illegible] re- [illegible] one rod per plot) throughout the floodplain. Depth was measured in August 1990 (pre-flood) and late March 1991 and May 1991 (post-flood). Fifteen of the rods could not be relocated after the flood. Relationships of sediment deposited or scoured by the 1991 flood with floodplain elevation (i.e., height above the water table), distance from the primary channel, and woody plant stem density were determined with univariate nonlinear regression analysis. Multivariate analysis was not utilized because variables were not independent (e.g., stem density and floodplain elevation). The relationship between average sedimentation within the floodplain and flow discharge was quantified with univariate regression, using data for the 1991 flood and for five smaller floods in prior years (Stromberg et al. 1991).

Tree and Shrub Survivorship and Recruitment

Stem density of woody plants was sampled within 100 permanent, nested plots distributed throughout the floodplain. Large trees (>10 cm stem diameter at a height of 1 m) were sampled in 1989 and after the flood in 1991 in 10 × 40-m plots. Density of shrubs, tree saplings (plants <1 cm stem diameter at a height of 1 m and >1 yr old), and pole trees (1–10 cm stem diameter at a height of 1 m) was sampled in late March or early April 1988, 1989, 1990, 1991, and again in

July or August 1991 in 2 × 2-m plots. Saplings, shrubs, and trees were mapped in all years, allowing for more precise calculation of post-flood revegetation and annual survivorship in years with different flood magnitudes. Tree and shrub seedling densities were measured monthly in 1991 in 4 × 4-dm plots to document post-flood seedling recruitment.

Survivorship of shrubs, saplings, and pole trees from 1990 to 1991 was analyzed in relation to several environmental variables (stem density, floodplain elevation, and distance from the channel; and water depth, velocity, tractive shear stress, stream power, and sediment deposited during the 1991 flood) with nonlinear regression analysis. The flood flow parameters were calculated from a calibrated HEC-2 floodplain model, and floodplain elevation and distance from the channel were determined from cross-sectional surveys of the floodplain (Stromberg et al. 1991). Survivorship was analyzed for a composite data set of all shrub, sapling, and pole tree stems, and separately for three individual species (*P. fremontii*, *S. gooddingii*, and *B. salicifolia*). Survivorship was not analyzed for species with low mortality (e.g., *P. velutina* and *Z. obtusifolia*) or those in fewer than 20 study plots (e.g., *H. monogyra* and *T. sericea*).

Herbaceous Cover

Cover of herbaceous vegetation was estimated visually within 100 permanent plots (1 × 1 m) distributed among several different overstory vegetation types. Herbaceous cover in four overstory types (*B. salicifolia* stands, *H. monogyra* stands, *Populus-Salix* forests, and *P. velutina* forests) was sampled in March and September 1988, 1989, 1990, and 1991. Cover in the streamside herbaceous type was sampled monthly during these years to document rates of post-flood recovery. To compare within-year effects of flooding, herbaceous cover by species was sampled in ten 1 × 1-m plots in flooded and unflooded *P. velutina* forests in March, April, June, and July 1991. Depth of sediment was used as the indicator of flooding. *Prosopis velutina* forests were chosen for this analysis because they occupied the highest floodplains and encompassed areas with and without flood impact. Mean cover and species richness per plot were statistically compared between flooded and unflooded forests with Student's *t* test.

Fig. 2. Daily hydrograph of the Hassayampa River during the 1990–91 water year. Data for 12–26 March were not available.

RESULTS

Flow Data and Floodplain Topography

The 1991 flood had peak discharge of 368 m^3s^{-1} on 1 March (Fig. 2), a value about 3000 times greater than the base flow rate (0.1 m^3s^{-1}), about 12 times greater than the 1.5-yr bankfull discharge (30 m^3s^{-1}), and with a recurrence interval of slightly less than 10 years (Jenkins 1989a). Discharge remained above base flow values through mid-April. The flood inundated nearly all of the floodplain, in contrast to a 5-year return flow that did not inundate high floodplains vegetated by *P. velutina* (Table 1). Peak flow velocity in the riparian zone in March 1991, as calculated from the HEC-2 floodplain model, ranged from 1.7 ± 0.6 m s^{-1} in the near-stream herbaceous vegetation type to 0.9 ± 0.4 m s^{-1} in the high floodplain *P. velutina* forests. For these same areas, peak water depth was 2.6 ± 0.2 m and 0.5 ± 0.3 m (Table 1); and tractive shear stress was 12.7 ± 7.3 kg m^{-2} and 3.4 ± 3.4 kg m^{-2}.

Surface topography was altered during the flood as a result of deposition of sediment and woody debris on floodplains, scouring of sediment from channel banks, and creation of scour pools along the main channel and in overflow channels. The 10-year return flood deposited more than twice as much sediment (8 cm) as a prior 5-year return flood (3 cm) (Fig. 3). Deposition peaked (maximum of 47 cm) on floodplain sites that were 1–2 m above the water table and declined in "bell curve" fashion on higher and lower surfaces (Fig. 4). This pattern differed from that for smaller prior-year floods in which [illegible] floods of varying recurrence intervals.

[illegible]	[illegible]	[illegible]	Flow velocity (m s^{-1}) 2-year flood	5-year flood	10-year flood
[illegible]	[illegible]	[illegible]	5.2 ± 2.0	6.0 ± 2.7	5.5 ± 1.9
[illegible]	[illegible]	[illegible]	3.8 ± 2.3	5.2 ± 3.4	5.4 ± 2.2
[illegible]	[illegible]	[illegible]	1.9 ± 0.6	2.7 ± 0.7	3.3 ± 1.0
[illegible]	[illegible]	[illegible]	2.2 ± 1.6	3.4 ± 2.4	3.6 ± 1.7
[illegible]	[illegible]	[illegible]	2.3 ± 1.2	2.6 ± 0.3	3.2 ± 1.2
[illegible]	[illegible]	[illegible]	2.4 ± 1.3	3.4 ± 1.3	3.5 ± 1.2
[illegible]	[illegible]	[illegible]	0.0 ± 0.0	0.0 ± 0.0	3.0 ± 1.4

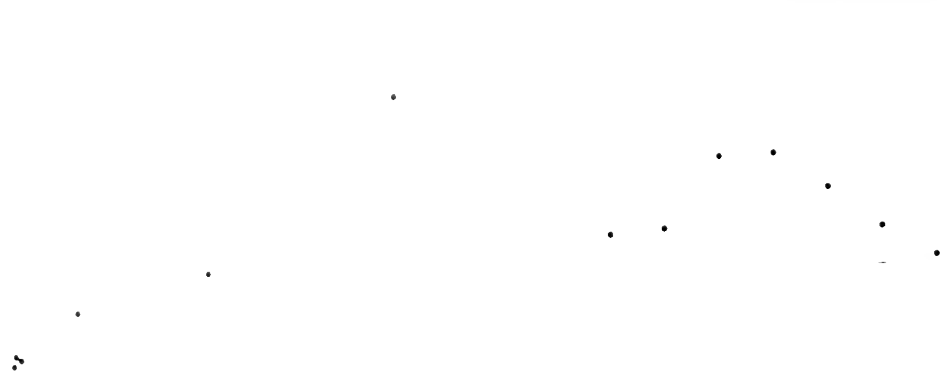

FIG. 4. Sediment deposition (means and standard deviations) [illegible] floodplains at various heights above the water table during [illegible]-year return flood in 1991 in the Hassayampa [illegible].

[illegible] linearly with increas- [illegible] Stromberg et al. 1991). [illegible] high adja- [illegible] loss of sedi- [illegible] regained [illegible] surges in [illegible] and shal- [illegible] again [illegible]

tion. Vegetation types with abundant woody stem density (e.g., *B. salicifolia* and *P. fremontii–S. gooddingii* pole stands) accumulated more sediment than did types with lower stem density (e.g., *H. monogyra* stands) (Table 2).

Tree and Shrub Survivorship

Woody plants growing on high floodplains where flood impacts were least had highest survivorship of the 1991 flood. For the composite sample of shrubs, saplings, and pole trees, survivorship increased significantly as functions of flood water depth (Fig. 5), floodplain elevation, and distance from the primary channel (Table 4). Mature trees of *P. velutina*, *P. fremontii*, and *S. gooddingii* grew on floodplains higher than 2 m above the water table and had 100% survivorship (Table 3). Saplings of *P. velutina* grew primarily in the understory of *P. fremontii–S. gooddingii* stands and also had high survivorship

TABLE 2. Depth of sediment deposited or scoured on the Hassayampa River floodplain during floods of varying recurrence intervals, by vegetation type. Mean floodplain height above the water table, distance from the stream channel, and density of woody stems are indicated for each vegetation type. Values are means ± standard deviation.

	Height above water table (m)	Distance from channel (m)	Woody stem density (no./m^{2})	Sediment (cm)		
				2-year flood	5-year flood	10-year flood
Streamside herbaceous	0.4 ± 0.1	4 ± 4	2.3 ± 2.7	9.8 ± 2.7	12.8 ± 4.7	11.2 ± 11.0
Populus-Salix saplings	0.7 ± 0.3	9 ± 8	9.9 ± 12.5	4.3 ± 4.3	5.4 ± 3.0	10.0 ± 6.2
Baccharis salicifolia	1.0 ± 0.5	22 ± 16	4.8 ± 4.9	2.7 ± 3.0	5.8 ± 5.7	13.4 ± 12.2
Populus-Salix poles	1.3 ± 0.5	22 ± 21	8.9 ± 4.6	4.2 ± 4.9	5.1 ± 4.2	14.7 ± 12.5
Hymenoclea monogyra	2.0 ± 0.5	35 ± 9	2.0 ± 2.1	0.9 ± 1.8	0.9 ± 1.1	5.8 ± 5.4
Populus-Salix forest	2.2 ± 0.7	48 ± 23	0.3 ± 0.8	0.3 ± 1.3	1.7 ± 2.6	7.8 ± 8.2
Prosopis velutina forest	2.7 ± 0.6	72 ± 20	0.4 ± 0.2	0.0 ± 0.0	0.6 ± 1.6	2.3 ± 4.2

(82%). Pole trees of *S. gooddingii*, *P. fremontii*, and *T. pentandra* grew on mid-height floodplains 1–2 m above the water table and had respective survivorship of 93%, 73%, and 38%. *Tamarix pentandra* was the only one of these three species that had much lower survivorship of pole trees in 1991 than in prior years. Saplings of these three species grew on floodplains <1 m above the water table, and each had about 35% survivorship of the 1991 flood.

Survivorship of the 1991 flood by poles and saplings of *P. fremontii* was significantly related to floodplain elevation, distance from the stream, and depth of floodwater (Table 4). *Salix gooddingii* survivorship showed the same trends, but relationships were not significant. *Populus fremontii* poles on floodplains 1–2 m above the water table had 94% ± 10 survival, compared to 60% ± 40 for those on floodplains <1 m high; values for saplings were 54% ± 46 for the higher floodplains and 30% ± 38 for the lower. With respect to flood water depth, *P. fremontii* and *S. gooddingii* poles and saplings showed a threshold-type response in which survivorship declined sharply where water was >1.5 m deep (Fig. 6). Sediment deposition, shear stress, stream power, and velocity were not significantly related to survivorship for either species. Between years, annual survivorship for *P. fremontii* and *S. gooddingii* saplings decreased significantly as annual maximum flood magnitude increased, with, for example, 30% of *P. fremontii* saplings surviving the 1991 flood, 43% surviving the 5-year return flood in 1988, and 58% surviving during the 1-year return flood year in 1989 (Fig. 7). In all years, *S. gooddingii* saplings had greater survivorship than *P. fremontii* saplings.

Fig. 5. Survivorship of riparian shrubs, saplings, and small trees (poles) in the Hassayampa River floodplain, 1990–91, in relation to flood water depth classes.

Survivorship by shrub species in 1991 corresponded to topographic position in the floodplain. Stem survivorship averaged 100% for *Ziziphus obtusifolia*, a species that grew on high floodplains (3.2 ± 0.6 m above the water table) vegetated by *Prosopis velutina* forests; >80% for *H. monogyra*, a species that grew on floodplains averaging about 2 m above the water table; and <20% for *T. sericea*, a low-floodplain species (1.3 ± 0.2 m) that sustained much stem breakage. Stem survivorship averaged 50% for *B. salicifolia*, the most abundant shrub in the floodplain. This species formed dense stands primarily on low floodplains (ca. 1 m high) but also grew in lesser densities on higher floodplains. Stem survivorship of *B. salicifolia* was not significantly correlated with any flood parameter.

[illegible] trees and shrubs in the Hassayampa River floodplain. Data are for [illegible] (1989–90), and 10-year return flood (1990–91).

[illegible]		Survivorship (%) 1988–89	1989–90	1990–91
[illegible]	[illegible]	NS[1]	NS	100
[illegible]	[illegible]	NS	NS	100
[illegible]	[illegible]	NS	NS	100
[illegible]	[illegible]	100	91	100
[illegible]	pole tree	87	80	93
[illegible]	pole tree	86	89	73
[illegible]	pole tree	95	87	38
[illegible]	sapling	76	87	82
[illegible]	sapling	64	78	36
[illegible]	sapling	13	58	30
[illegible]	sapling	84	75	37
[illegible]	shrub	100	100	100
[illegible]	shrub	96	100	83
[illegible]	shrub	100	100	51
[illegible]	shrub	100	100	17

[1] [illegible] sapling [illegible] stems [illegible] 1 cm diameter and are greater than 1 year in age.

[illegible] regression coefficients [illegible] values [illegible] relating [illegible] parameters to survivorship of a 10-year return flood [illegible] Hassayampa River [illegible] saplings and pole trees of [illegible] and *Salix gooddingii* and by a composite [illegible] saplings, and pole trees.

	Distance from channel	Height above streambed	Water depth during flood
[illegible]	0.20	0.25	0.45
[illegible]	0.02	0.10	0.10
[illegible]	0.11	0.15	0.13

[illegible] Revegetation

[illegible] period of *P. fremontii* [illegible] with the period of [illegible]. As a result, *P. fremontii* [illegible] and broad [illegible]. In April, [illegible] up to [illegible] m [illegible] dessication. By the end of summer there were 5 seedlings m^{-2} on floodplains <1 m above the water table (Table 5), a value sufficiently high to eventually produce a mature forest with characteristic density of 0.3 stems m^{-2} (Table 2). *Salix gooddingii* seedlings also germinated abundantly in 1991 after the flood pulse. In May 1991 there were 618 *S. gooddingii* seedlings m^{-2} in plots <1 m above the water table (Table 5). Seedlings by the end of summer were most abundant on floodplains 0.4–0.6 m above the water table. *Tamarix pentandra* germinated in June–September, after *P. fremontii* (March–April) and *S. gooddingii* (April–May). *Tamarix pentandra* had maximum seedling density of 5 ± 13 m^{-2} in June 1991, but none were alive by the end of summer.

Baccharis salicifolia stems recovered to pre-flood densities (4.8 ± 4.5 m^{-2}, measured within *B. salicifolia* vegetation zones) by July 1991, primarily a result of stem sprouting and in part a result of seedling recruitment. Stem density of *Hymenoclea monogyra* increased by late summer 1991 to a value somewhat higher than pre-flood levels (2.3 ± 2.5 stems m^{-2}) as a result of vegetative reproduction. *Tessaria sericea* also had post-flood vegetative spread, but stem densities had not attained pre-flood levels by late summer.

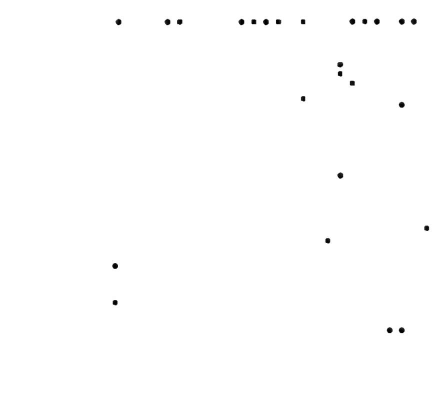

Fig. 6. Survivorship of saplings and small trees (poles) of *Populus fremontii* and *Salix gooddingii*, 1990–91, in relation to maximum water depth during a 10-year return flood.

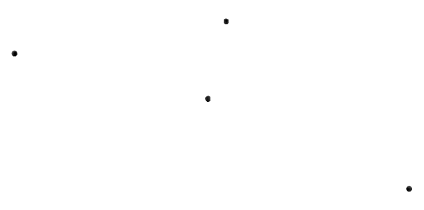

Fig. 7. Annual survivorship of saplings of *Populus fremontii* and *Salix gooddingii* along the Hassayampa River floodplain in relation to maximum annual flood flow rate. Regression equations are: $y = 59 - 0.08x$, $r^2 = .99$, df = 2, $P < .01$ (*P. fremontii*); and $y = 82 - 0.12x$, $r^2 = .97$, df = 2, $P < .05$ (*S. gooddingii*).

Fig. 8. Density of *Populus fremontii* in relation to water table depth, by month during 1991.

Herbaceous Cover

Spring herbaceous cover in all vegetation types except that of the highest floodplains (*P. velutina* forests) was less abundant in 1991 than in prior years (Table 6). Herbaceous cover under *P. fremontii–S. gooddingii* forests, for example, averaged 8% in 1991 compared to 25–43% in prior years. Herbaceous cover on streambanks and in *B. salicifolia* stands was 16% and 11% respectively in late March 1991 compared to 38% and 34% in the prior year. Cover in these two areas was composed primarily of rhizomatous grasses (the native *Paspalum distichum* and the exotic *Cynodon dactylon*) and also contained lesser amounts of other natives (e.g., *Typha domingensis* and species of *Juncus*) and exotics (e.g., *Melilotus albus* and *Polypogon monspeliensis*). Cover in these areas increased nearly to pre-flood levels by September. Cover within higher-elevation vegetation types (e.g., *Populus-Salix* forests) remained low as of late summer. Within *P. velutina* forests, areas that were flooded had lower cover but greater richness and diversity of species throughout the summer compared to areas that were not flooded (Table 7). Unflooded and flooded areas in the *P. velutina* forest were both initially dominated by two exotic winter-germinating annuals, *Hordeum leporinum* and *Sisymbrium irio*. These two species continued to dominate unflooded areas throughout spring and early summer. Flooded areas, in contrast, had about 1/6th the cover of unflooded areas, and about 4–5 times as many species (e.g., 9.2 ± 1.9 m^{-2} vs. 1.9 ± 0.5 m^{-2}, April data). These included several native annual forbs (e.g., *Amaranthus palmeri*, *Bowlesia incana*, *Amsinckia intermedia*, *Gilia sinuata*, *Lotus humistratus*, *Microseris linearifolia*, *Xanthium strumarium*, and *Verbesina encelioides*) and several exotic annual forbs and grasses (e.g., *Bromus rubens*, *Herniaria cinerea*, *Solanum rostratum*, and *Tribulus terrestris*).

DISCUSSION

Riparian systems are noted for their resiliency, i.e., the ability to quickly return to pre-disturbance conditions. Rapid growth rates, high fecundity, and capacity for asexual reproduction are among the factors that allow rapid recovery [illegible] during the period of maximum abundance and at the end of the growing [illegible] Hassayampa River floodplain surfaces < 1 m above the water table.

	[illegible]		*Salix gooddingii*		*Tamarix pentandra*	
	[illegible]	October	May	October	June	October
[illegible]	[illegible]	0	385	0	11	0
[illegible]	[illegible]	0	2	0	< 1	0
[illegible]	0	0	< 1	0	0	0
[illegible]	[illegible]	5	618	3	5	0

[illegible] Herbaceous cover [illegible] along the Hassayampa River floodplain, by vegetation type, from 1988 to 1991. Values [illegible] standard deviation.

		1988	1989	1990	1991
[illegible] herbaceous	March	20 ± 24	29 ± 36	38 ± 31	16 ± 31^d
	April	38 ± 26	66 ± 28	68 ± 30	29 ± 37
	May	38 ± 25^d	68 ± 28	72 ± 29	35 ± 41
	July	66 ± 22	74 ± 30	43 ± 30^d	41 ± 38
	Sept	69 ± 34	77 ± 30	60 ± 25	60 ± 35
[illegible] salicifolia shrubland	March	22 ± 18	19 ± 19	34 ± 26	11 ± 24^d
	Sept	38 ± 36	41 ± 35	25 ± 21	41 ± 43
[illegible] monogyra shrubland	March	19 ± 16	20 ± 21	24 ± 21	4 ± 4^d
	Sept	7 ± 11	15 ± 13	12 ± 11	13 ± 13
[illegible]-Salix forest	March	43 ± 27	25 ± 21	34 ± 31	8 ± 12^d
	Sept	19 ± 29	21 ± 28	21 ± 23	5 ± 6
[illegible] velutina forest	March	81 ± 17	35 ± 21	58 ± 26	52 ± 45^d
	Sept	7 ± 12	12 ± 16	10 ± 17	6 ± 13

[illegible] richness, and Shannon-Weiner diversity of herbaceous understory species in *Prosopis velutina* forests [illegible] not inundated during a 10-year return flood in March 1991. Values for cover and richness are means ± [illegible]

	Cover (%)		Species richness		Species diversity	
[illegible]	Flood	No flood	Flood	No flood	Flood	No flood
[illegible]	[illegible]	71 ± 30	2.3 ± 0.5	1.9 ± 0.6	0.53	0.91
[illegible]	[illegible]	79 ± 36	9.2 ± 1.9	1.9 ± 0.5^c	2.16	0.73
[illegible]	[illegible]	84 ± 24	10.1 ± 3.1	2.2 ± 0.8^c	2.53	0.45
[illegible]	[illegible]	88 ± 11	7.9 ± 3.0	2.6 ± 2.3^c	2.31	1.23

[illegible] Stromberg [illegible] 1990). [illegible] floodplain [illegible] stems also [illegible] floods [illegible] or [illegible] and Minckley 1981).

The 10-year return flood in the Hassayampa River inundated most of the floodplain and deposited a net average of 8 cm of sediment (maximum of 0.5 m). Low-elevation floodplain surfaces had greatest flow velocities (to 7 m s^{-1}) and water depths (to 2.8 m). The native riparian vegetation showed a mixture of resistance and resilience to this flood disturbance. Species on high floodplains (e.g., *P. velutina* and *Z. obtusifolia*) had no mortality, while those on lower-elevation floodplains variously had mortality followed by seedling recruitment (*P. fremontii* and *S. gooddingii*) or by vegetative reproduction (e.g., *Baccharis salicifolia*).

Prosopis velutina was the dominant tree on high floodplains (ca. 3 m above the water table) and had high survivorship of trees and saplings. It did not show post-flood seedling recruitment, consistent with prior studies indicating that *P. velutina* seeds germinate primarily after late summer floods (Stromberg et al. 1991). *Populus fremontii* and *S. gooddingii* trees grew on floodplains 2–3 m high and also had high survivorship. Young trees and saplings of these two species were on younger, less aggraded floodplains and sustained some mortality. *Salix gooddingii* saplings and poles had lower mortality than did *Populus fremontii*, perhaps because of greater stem pliability and tolerance to saturation (McBride and Strahan 1984, Hunter et al. 1987). Survivorship of both species was greater on sites where flood waters were shallowest, a factor reported to be an important determinant of flood survivorship in other riparian systems (Stevens and Waring 1988). The relationship between water depth and survivorship may be an expression of effects of flood hydraulic force on plant removal or mortality via abrasion and stem breakage, rather than of a causal relationship between root saturation and mortality. Although correlations of mortality with flood velocity and shear stress were not statistically significant, this may have been due to chaotic movement of water and sediments on the floodplain, which are not adequately represented by flood-simulation models such as HEC-2.

The 1991 flood created optimal seedling recruitment conditions for *Populus fremontii* and *Salix gooddingii* by scouring channel banks and depositing new sediment on stream banks, reducing herbaceous and overstory competition (at least temporarily), and moistening floodplains at an appropriate time (during seed dispersal) and place (moderately high surfaces above the zone of frequent summer flood scour) (Stromberg et al. 1991). Tree-ring studies have shown that *P. fremontii* and *S. gooddingii* establish in large scale about once a decade within the Hassayampa River system, during or after years with large flows (>250 m^3s^{-1}; 7-year return flood) (Stromberg et al. 1991). This present study confirms the role of large floods in increasing age-class diversity for these episodically recruiting species.

The exotic *T. pentandra* co-occurred with *Populus* and *Salix* but had greater mortality of pole trees than did the native trees. Mortality of *T. pentandra* more likely resulted from intolerance to physical flood effects than from physiological intolerance to inundation (Warren and Turner 1975, Irvine and West 1979). *Tamarix pentandra* had low post-flood seedling establishment, due in part to a low density of mature seed-producing trees in the Hassayampa floodplain and in part to the fact that the flood occurred several months prior to *T. pentandra* seed germination and thus did not moisten potential germination sites at an appropriate time (June through October). Additionally, much of the available "germination space" during its germination period was preempted by herbaceous cover and by seedlings of *P. fremontii* and *S. gooddingii*, species that precede *Tamarix pentandra* in the chronosequence of tree species germination at the Hassayampa River.

Vegetative reproduction is a common post-disturbance revegetation mechanism in floodplain systems (Gecy and Wilson 1990) and was demonstrated by all shrub species in the Hassayampa River floodplain that had flood mortality. Extent of flood mortality of shrub species at the Hassayampa varied with their topographic position in the floodplain. *Zizyphus obtusifolia*, a species of high floodplains (ca. 3 m above the water table), had no mortality. *Baccharis salicifolia* underwent a 50% decline in stem density during the flood but increased to pre-flood densities by late summer primarily via stem sprouting. *Hymenoclea monogyra* and *T. sericea* are both clonal shrubs that spread via root sprouts after mechanical injury (Gary 1963) and via shoot sprouts after stem burial. *Hymenoclea monogyra* compensated for flood mortality by vegetative reproduction; but this was not the case for *Tessaria sericea*, a low-floodplain species that had high flood mortality. Other studies also have reported low flood survivorship for *Tessaria sericea* (Stevens and Waring 1988).

Vegetative reproduction also was the dominant revegetation method for herbaceous plants along stream banks and low-elevation floodplains. Cover in these areas declined by about half after the flood but recovered to pre-flood levels by late summer. Flood-tolerant perennial [illegible] commonly *Dacty-* [illegible] and prior to the flood [illegible] of high flow [illegible] may ultimately [illegible] predominance during flood-[illegible] periods (Fisher et al. 1982, Hen-[illegible] Minckley 1981). Understories of higher elevation floodplains showed changes in cover and composition after the 1991 flood. Prior to the flood, *P. velutina* forests were dominated by dense, nearly monotypic stands of exotic annual species (e.g., *Hordeum murinum*) that probably had become established during past years of cattle grazing and other exogenous disturbances (Wolden et al. 1991). After the flood these areas had lower cover but greater richness of herbaceous species and greater relative abundance of native annuals. We speculate that compositional changes were due to reduced competition with entrenched exotics, an influx of flood-borne seeds from upstream areas or other vegetation types within the floodplain, or altered edaphic conditions resulting from deposition of sediment with different texture or nutrient content (Stevens and Waring 1988).

Fluvial processes including floodplain aggradation and formation of microrelief patterns (e.g., backwater depressions) contribute to the diversity and "mosaicism" of riparian plant communities in many flood-driven ecosystems (Kalliola and Puhakka 1988). Within the Hassayampa floodplain, as well, variable sediment deposition and scour patterns contributed to "patchiness" within the riparian floodplain. For example, localized light gaps were formed in areas with major debris deposition, and scour pools (i.e., backwater depressions) were formed along main channels and in overflow channels. Floodplain sedimentation accentuated the existing hydrological gradients (e.g., gradients in depth to groundwater), which contribute to [illegible] riparian ecosystems of [illegible] and elsewhere (Hupp [illegible] 1987, Bravard et al. 1986).

[illegible] resulted in greater [illegible] greater woody plant [illegible] floods. Effects of [illegible] can only be spe[illegible] flood in 1970 [illegible] 1980a) appare[illegible] ripar-ian vege[illegible] of extensi[illegible] that established in 1959, 1952, and earlier (Stromberg et al. 1991). The 10-year return flood probably reached a "geomorphic threshold," that being the level at which substantial change in floodplain morphology and vegetation begins to occur, based on studies of other desert rivers that implicate the 5-year return flow as a threshold discharge for channel and floodplain instability (Graf 1983).

Other potential effects of the flood on riparian vegetation such as changes in plant productivity as a result of nutrient or water pulses were not addressed in this study, nor was the role of vegetation in moderating flood processes explicitly addressed.

Data in this paper suggest that floodplain vegetation aided in stream bank stabilization and sediment trapping, important functions of wetland and riparian vegetation (Fisher and Minckley 1978, Cooper et al. 1987, Sullivan and Stromberg 1992). The vegetation also may have enhanced groundwater recharge and reduced the downstream impact of flood flows by reducing flow velocities and increasing water retention time within the floodplain (Burkham 1976, Beschta and Platts 1986).

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HABITAT SELECTION OF MERRIAM'S TURKEY (*MELEAGRIS GALLOPAVO MERRIAMI*) HENS WITH POULTS IN THE BLACK HILLS, SOUTH DAKOTA

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ABSTRACT—We studied habitat selection patterns of Merriam's Turkey (*Meleagris gallopavo merriami*) hens with poults in a ponderosa pine (*Pinus ponderosa*) ecosystem. Thirty-six radio-marked hens produced 19 broods, and we obtained 230 locations of hens with poults. We described vegetation of habitats using criteria from the Rocky Mountain Region, U.S. Forest Service, for determining effects of forest management and monitoring of wildlife populations. Most habitat units were 4–32 ha and corresponded to third-order habitats as described by Johnson (1980). Hens with poults selected large meadows and rarely selected dense ponderosa pine habitats. Younger poults used meadows more frequently than did older poults. Implementation of the Black Hills National Forest Land and Resource Management Plan in ponderosa pine habitats will not negatively impact hens with poults. Grazing by livestock reduces herbaceous biomass necessary for invertebrate food items of poults and cover for poults. Habitat selection patterns of hens with poults should be evaluated by age categories of poults.

Key words: Merriam's Turkeys, Meleagris gallopavo merriami, *poults, habitat selection, forest management, invertebrates, meadows, radio telemetry, grazing.*

Merriam's Turkeys (*Meleagris gallopavo merriami*) historically ranged as far north as southern Colorado when settlers moved into the southwestern United States (MacDonald and Jantzen 1967). In 1948, 1950, and 1951, wild turkeys were transplanted to the Black Hills of South Dakota in three separate releases of 8, 15, and 6 birds, respectively (Petersen and Richardson 1973). By 1952, estimated turkey populations in the Black Hills of South Dakota and Wyoming were 1000 birds, and by 1960 population estimates were 5000–7000 birds (Petersen and Richardson 1973), suggesting excellent reproductive potential in habitats of this region.

Current pressures from society and statutory mandates (e.g., National Forest Management Act, Renewable Resources Planning Act, National Environmental Policy Act) require that the effects of management activities such as grazing and timber harvest on the various wildlife species be considered in management decisions. Recently, the value of ponderosa pine has increased, placing greater demands for logging in the Black Hills (G. Gire, silviculturist, Black Hills National Forest, personal communication). Increased value of timber resources, emphasis on old-growth timber values, and improvements in technology of harvesting timber have renewed concern for the habitat requirements of Merriam's Turkeys (Shaw 1986). In addition to loggers, other users also are increasing their awareness and use of national forest lands.

The objective of this study was to describe habitat requirements of turkey poults in a ponderosa pine ecosystem at the same resolution level as that used by the U.S. Forest Service in making management decisions and monitoring the effects of those decisions on wildlife.

METHODS

Study Area

This study was conducted in the central Black Hills of South Dakota, approximately 16 km west of Rapid City. Most of the land is under management of the Black Hills National Forest, Pactola Ranger District, although private holdings associated with ranch operations and several private homes and cabins exist in the study area.

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Vegetation in the study area is primarily pure ponderosa pine forest (84%). Meadows and aspen (*Populus tremuloides*)/birch (*Betula papyrifera*) habitats occur in drainages, but some monotypic aspen habitats also occur on north exposures. Bur oak (*Quercus macrocarpa*) and white spruce (*Picea glauca*) constitute less than 1% of the study area. Climax vegetation or potential natural communities include the following: *Pinus ponderosa/Symphoricarpos albus*, *P. ponderosa/Arctostaphylos uva-ursi*, *P. ponderosa/Juniperus communis*, *Populus tremuloides/Corylus cornuta*, *Quercus macrocarpa/Ostrya virginiana*, *Q. macrocarpa/S. albus*, and *Picea glauca/Linnaea borealis* types as described by Hoffman and Alexander (1987).

Geologic material is predominantly Precambrian and Cambrian granite, schists, and metasediments (Hoffman and Alexander 1987). Elevation ranges from approximately 1300 to 1800 m. Climate is continental, with cold winters and warm summers (Orr 1959). January is typically the coldest month, with mean temperature extremes of −11–2 C; July and August are the warmest, with mean temperature extremes of 15–29 C. Average annual precipitation is 50–55 cm, of which 70–80% falls between April and September (South Dakota Climatological Summary, No. 20-39-6, U.S. Weather Bureau). Snowfall averages 84 cm but may range from 25 to 200 cm.

Trapping and Locations

We trapped wild Merriam's Turkeys during late February or early March of 1986, 1987, and 1988 with rocket nets and drop nets over corn bait piles. Thirty-six females were fitted with backpack radio transmitters weighing approximately 108 g. Radio transmitters were attached to hens with 15.2-cm bungee cords looped under the wing.

Hens with poults were monitored until behavior or [illegible] pulse suggested the hen had [illegible]. After eggs hatched, radio-marked hens were located three times each week [illegible] to obtain one location in each of three time periods (sunrise to 0959, 1000–1500, [illegible]) each week. Turkey locations [illegible] plotting bearings from known [illegible] 1:24,000 contour maps in the [illegible] were usually taken from positions [illegible] the estimated location. Universal Transverse Mercator coordinates were recorded to the nearest 100 m for each location. Only one location was recorded for each bird on any given day. We considered observations of more than one radio-marked bird at a location as one observation to assure independence among observations (Alldredge and Ratti 1986). Each location of a hen with poults was assigned to a corresponding compartment and stand (see Habitat Descriptions below). We collected habitat use data of hens with poults over a three-year period, 1986–1989 during the months of June–September.

Habitat Descriptions

Habitats were determined by U.S. Forest Service criteria and assigned to numerically identified geographical units. Boundaries were defined by watershed topography (ridges and drainages) or distinct changes in vegetation type. Private lands in the study area were assigned to habitats based on interpretation of aerial photographs; boundaries of adjacent habitats were extended if the vegetation type was continuous. New boundaries were assigned if changes in vegetation were apparent. Typically, these habitats are 4–32-ha land units, although smaller-size habitats (inclusion habitats) were delineated if distinct vegetation types could be identified on 1:24,000 aerial photographs. Inclusion habitats were riparian areas, meadows, aspen/birch draws, and monotypic aspen communities. Five hundred thirteen habitat units encompassing 4380 ha were delineated on the study area.

Vegetative descriptions of each habitat unit were obtained from five plots uniformly assigned to each habitat unit and marked on 1:24,000 contour maps in the laboratory. Plots in each habitat unit were then located using these maps. Diameter breast height (dbh) of trees and tree basal area were estimated at each plot using a 10-factor prism (Sharpe et al. 1976). When habitat units were too small to effectively place five plots, fewer plots were used.

Habitat assignments were made based on dominant species of vegetation (DSV) and overstory canopy cover (OCC) (Buttery and Gillam 1984). Criteria for describing habitats allowed for further stratification by dbh, but the most useful resolution level in determining habitat selection patterns of turkeys included DSV and OCC (Rumble and Anderson 1992). DSV categories were ponderosa pine, aspen/birch, oak,

Table 1. Use and selection of habitats by Merriam's Turkey hens with poults in the central Black Hills, South Dakota. Habitats selected less ($P \leq .10$) than expected are indicated by −−, and those more than expected by ++.

Habitat	Percent canopy cover	Proportional area	Age			
			0–3 weeks (N = 106)[a]	4–7 weeks (N = 65)	8–12 weeks (N = 59)	0–12 weeks (N = 230)
Aspen/birch	0–40	0.0148	0	1	1	2
Aspen/birch	40–70	0.0191	2	1	0	3
Aspen/birch	70–100	0.0177	4	0	2	6
Oak	0–100	0.0044	3	0	0	3
Spruce	0–100	0.0056	1	0	0	1
Meadows		0.1016	36^{++}	17^{++}	9	62^{++}
Ponderosa pine	0–40	0.1199	16	7	5	28
Ponderosa pine	40–70	0.3760	31	32	29	92
Ponderosa pine	70–100	0.3412	13	7	13	33

[a] Sample sizes reported are the number of radio locations of hens with poults by age category.

spruce, and meadows. OCC categories were 0–40%, 41–70%, and 71–100% and were estimated based on the following equation: $OCC(\%) = 0.51*BASAL\ AREA(FT^2/AC) - 1.94$ (Bennett 1984). Nine habitat categories were determined. These habitats correspond to third-order habitats as described by Johnson (1980).

Analyses

Chi-square tests for independence were used to test the hypotheses that (1) habitat use patterns by hens with poults were similar among age categories of poults and (2) habitat use patterns by hens with poults were similar among time periods of the day. An evaluation of chi-square residuals with a G standardization to a critical Z statistic (Mosteller and Parunak 1985) was used to determine significant differences of habitat use among age categories of poults.

Chi-square goodness-of-fit tests corrected for continuity (Cochran 1963) were used to test the hypotheses that habitat selection patterns of hens with poults were similar to random expected use for (1) all hens with poults and (2) three age categories of poults. Confidence intervals around proportional use were used to determine habitats selected more or less than expected (Neu et al. 1974, Byers et al. 1984). Bonferroni-corrected Z statistics were compared to the standardized chi-square residual (Mosteller and Parunak 1985:198) to determine if habitat selection deviated from expected random use when <5 observations occurred in a habitat. Statistical significance for all tests was $\alpha = .10$.

We assured correct classification of the habitat at turkey locations in several ways. Habitat boundaries were marked on field maps. When the location of a hen with poults was near the habitat boundaries, we verified field location by walking around the radio-marked bird while continuously monitoring changing directions of the signal, and/or by obtaining visual locations without disturbing the bird. More than half of the 230 data points used for analyses were visual locations.

The term *habitat use* will be used when habitats in which turkeys were observed were not compared to availability; *habitat selection* will be used when habitats in which turkeys were observed were compared to availability (Thomas and Taylor 1990).

RESULTS

Thirty-six radio-marked hens in this study produced 19 broods from which habitat use and habitat selection patterns were evaluated. A total of 230 independent observations of habitat use were made. Smaller sample sizes of older age categories of poults (Table 1) were due to mortality and movements out of the defined study area.

Habitat use differed among age classes of poults ($P \leq .001$). Ponderosa pine habitats with 71–100% overstory canopy cover were used more by hens with 8- to 12-week-old poults than by younger poults. Ponderosa pine habitats with 0–40% overstory canopy cover were used relatively more by poults younger than 8 weeks than by older poults.

Habitat selection patterns of hens with poults differed significantly ($P < .001$) from random use patterns. Summed across all age categories, hens with poults selected meadow habitats more than expected, but rarely were observed in ponderosa pine habitats with >70% overstory cover. Habitat selection patterns of hens with poults younger than 8 weeks old were identical to those for all poults. No significant patterns of habitat selection were apparent for hens with poults 8–12 weeks old ($P \leq .11$).

Habitat use did not vary ($P = .51$) among the three daily time periods for all hens with poults. Nor did habitat use patterns vary ($P \geq .30$) among daily time periods when evaluated for individual age categories of poults. Meadow habitats selected by hens with poults were more than two times larger ($\bar{x} = 36 \pm 4$ ha, $P \leq .02$) than the average ($\bar{x} = 16 \pm 7$ ha) within the study area.

DISCUSSION

Edges of Kentucky bluegrass meadows best characterized habitats selected by hens with poults. Open ponderosa pine habitats with extensive understory vegetation were selected to a lesser degree. Hens with poults selected dense ponderosa pine habitats infrequently except as escape or occasional loafing cover. Hens with poults in meadows were seldom observed more than 10 m from the forest-meadow edge.

Use of forest meadows or forest-meadow ecotones by hens with broods is common for nearly all subspecies of turkeys (Jonas 1966, Hillestad and Speake 1970, Williams et al. 1973, Scott and Boeker 1975, Speake et al. 1975, McCabe and Flake 1985, Day et al. 1991). Hens with poults in this study selected the largest Kentucky bluegrass meadows (2–188 ha) and rarely selected small clearings in the forest or upland dry meadows. Small openings and upland dry meadows are common on the study area, often occurring within 200 m of Kentucky bluegrass meadows selected by hens with poults. These upland dry meadows in the Black Hills are less productive than Kentucky bluegrass meadows (Hoffman 1973). Healy and Nenno (1983) found that poults prefer natural clearings in the forest over artificial openings. Findings from this study contradicted results reported for Merriam's Turkeys in other regions; Schemnitz et al. (1985) and Mackey (1986) both noted poults using openings less than .25 acre). Hengel (1990) reported hens with poults in Wyoming using riparian areas and meadows. In this study several hens with poults 2–4 days old moved long distances to large meadows. One hen took her brood 5.6 km (3.5 miles) in less than 4 days to a large meadow, and another moved approximately 1.8 km in less than 2 days to the same meadow. The longest movement by a hen with poults was more than 23.4 km over a 6-week period. They went to the same large Kentucky bluegrass meadow as the previous two. Day et al. (1991) reported direct movements of up to 3.5 km from nests to centers of habitat for turkey broods.

Hens with poults select meadows or other habitats because herbaceous vegetation supports an abundance of invertebrates. Invertebrates are necessary in diets of young gallinaceous birds for proper growth and survival (Johnson and Boyce 1990). Invertebrate abundance in this study area was greater in meadows than in other habitats (Rumble 1990). Poults have high protein requirements during the 4 weeks after hatching (Robbins 1983, Hurst and Poe 1985). Based on changes of habitat selection patterns presented here, use of meadow habitats and subsequent feeding on invertebrates continued through 7 weeks of age. Grazing by livestock reduces the herbaceous cover and associated invertebrate abundance. Habitat selection and survival of poults are correlated with abundance of herbaceous cover (Metzler and Speake 1985). Therefore, excessive grazing by livestock would be detrimental to poults less than 7 weeks old.

Habitat selection patterns of poults changed as the poults became older. Proportional use of meadows declined from 34% for poults less than 4 weeks old, to 26% for poults 4–7 weeks old, and 15% for poults older than 8 weeks. Similar trends in habitat selection patterns have been noted for Merriam's Turkeys and other subspecies of wild turkeys (Pack et al. 1980, Healy and Nenno 1983, McCabe and Flake 1985, Campo et al. 1989). Increased selection of forested habitats may be related to lower requirements for protein following feather development (Robbins 1983). Increased selection of forested stands with >40% overstory canopy cover by poults older than 7 weeks is within the range of overstory canopy cover management of ponderosa pine directed in the Black Hills National Forest Land and Resource Management Plan (Forest Plan). The Forest Plan calls for management of pine stands to 60 or 80 growing stock level (GSL). GSL is the basal area of a stand projected to 25 cm dbh trees (Boldt and Van Duesen 1974).

Because of changing habitat selection patterns of hens with age of poults, habitat requirements of wild turkey hens with poults should be assessed by age categories of poults. Including poults older than 8 weeks in analyses of younger poults can obscure some habitat relationships.

MANAGEMENT IMPLICATIONS

Because hens with poults selected meadows during critical growth and development phases of poults (<7 weeks), and because older poults selected forest stands with >40% overstory canopy cover, managing ponderosa pine stands to 60 or 80 GSL would not negatively impact habitats of hens with poults. However, dense ponderosa pine stands (>100 ft^2/ac basal area) should be left along meadow edges to provide escape and loafing cover for hens with poults. Grazing by livestock reduces the standing biomass of herbaceous vegetation in meadows; excessive grazing would also reduce the abundance of invertebrates and cover necessary for growth and development of poults.

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SQUIRRELS AS PREDATORS

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ABSTRACT.—A literature review and field observations indicate that most sciurids are facultative predators on small vertebrates. This behavior is documented for at least 30 sciurid species in 8 genera. The frequency of predation apparently is influenced by various factors including climate, season, gender, reproductive condition, and availability of plant sources for certain nutrients such as calcium and nitrogen. Although sciurids assimilate as much energy from animal foods as do obligate carnivores, behavior associated with predation appears to be less efficient in sciurids and may rely partly on prey habituation and other adaptive behaviors.

Key words: squirrel, Sciuridae, predator, carnivore, omnivore.

Predators utilize various strategies that maximize the probability of successful prey capture while minimizing the probability of injury. Sciurid rodents, many of them facultative and opportunistic predators, are not morphologically specialized for this role and should therefore possess a wide variety of adaptive attack behaviors. As discussed below, one of these behaviors observed in tree squirrels appears similar to insinuation (Curio 1976), a strategy more often associated with invertebrates than with mammals.

Predation, as defined here, means the killing and eating of active vertebrates (including conspecifics) or other relatively large, mobile prey by free-living squirrels. This definition excludes the consumption of eggs, nestling birds, small insects, or any animal that is already dead. Prey offer some resistance; eating carrion or aphis is similar to browsing. Predation also excludes killing that appears unrelated to feeding, as in defense of the nest (Harris 1985) or as a reproductive strategy (Balfour 1983, Weissenbacher 1987). Finally, behavior of caged squirrels is often abnormal and is excluded here as evidence of predation, although it can provide clues to dietary deficiencies.

Not all biologists accept the idea of squirrels as frequent predators. Despite the 70-year literature record summarized in Table 1, O'Donoghue's recent (1991) finding that squirrels are the chief predator of juvenile snowshoe hares elicited general "shock" (C. Krebs, personal communication). There is universal acceptance that squirrels eat meat; the question is how they obtain it. Squirrels are often seen eating carrion on roads but are rarely seen attacking live prey. Stomach contents analysis may overlook vertebrate flesh and cannot distinguish live prey from carrion. Thus, each new observation of a squirrel acting like a predator becomes a journal note (see Literature Cited). Although most of these notes imply that such behavior is aberrant, collectively they describe a significant component of the sciurid repertoire. The same feeding adaptations that enable squirrels to crack nuts are sufficient for opening skulls (Landry 1970).

TREE SQUIRRELS.—The following field observation (which prompted this review) adds a species to the list of reported sciurid predators. On 6 April 1979, I saw a lactating female western gray squirrel (*Sciurus griseus*) stalk and attack an adult mountain quail (*Oreortyx pictus*) in mixed-conifer forest at Black Mountain, Riverside County, California, elevation 1800 m. The quail was standing on a 60-cm stump at the edge of a clearing; five or six other quail were nearby. None of the quail appeared to react as the squirrel crossed the clearing in an odd, crouched posture, rustling the pine needles and leaves loudly enough to attract my attention. When it was 20 cm from the stump, it leapt up and pounced on the quail. After a brief struggle, the quail escaped and the covey moved off. In six years in the same area, on two other occasions

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[illegible] This table is limited to behavior of free-living squirrels and includes [illegible] in text

[illegible]	[illegible]	Source
[illegible] squirrel *S[illegible]*	Conspecifics, birds	Holm (1976), Bailey (1923)
[illegible] squirrel *[illegible]*	Mountain quail, unidentified small mammal (*Peromyscus*?)	This paper
[illegible] squirrel *[illegible]*	Dove, blue jay, other birds	Borell (1961), Seton (1929), Shaffer and Baker (1991)
European red squirrel *Sciurus vulgaris*	Squirrels, birds	Gurnell (1987), Schlogel (1985)
[illegible] squirrel *[illegible]*	Ground squirrels	Roest (1951)
[illegible] Red squirrel *Tamiasciurus hudsonicus*	Chipmunks, tree squirrels, cottontail, snowshoe hare, mourning dove, other birds	Hatt (1929), Seton (1929), Hamilton (1934), O'Donoghue (1991), Nero (1987), Taylor (1988)
[illegible] green squirrel *[illegible] poensis*	Frog (live?)	Emmons (1980)
GROUND SQUIRRELS		
White-tail antelope squirrel *Ammospermophilus leucurus*	Pocket mouse, kangaroo rat, lizards	Bradley (1968), Morgart (1985)
Nelson antelope squirrel *Ammospermophilus nelsoni*	Lizards	Hawbecker (1947)
Yellow-bellied marmot *Marmota flaviventris*	Conspecifics	Armitage et al. (1979)
California ground squirrel *Spermophilus beecheyi*	Ground squirrels, rabbits, pocket gophers, moles, birds, lizards	Grinnell & Storer (1924), Fitch (1948), Sumner & Dixon (1953), Sandberg and Banta (1973), Trulio et al. (1986)
Belding ground squirrel *Spermophilus beldingi*	Chipmunks, other small mammals, junco, warbler	Sharsmith (1936), Howell (1938), Sherman & Morton (1979), Michener (1982)
Souslik *Spermophilus citellus*	Field mice, birds, snakes, conspecifics	Calinescu (1934), Herzig-Straschil (1976)
[illegible] ground squirrel *[illegible]*	Fish (live?)	Howell (1938)
[illegible] ground squirrel *[illegible]*	Voles, domestic fowl, ducks, other birds	Polder (1955), Johnson (1922), Howell (1938), Sowls (1948), Choromanski & Sargeant (1982)
[illegible]	Voles, deer mice, chipmunks, junco, lizards	Cameron (1967), Tevis (1953)
[illegible]	Cottontail	Packard (1958)
[illegible]	Sparrows	Bradley (1968)
[illegible]	Conspecifics	Michener (1982)
[illegible]	[illegible] birds	Bridgewater & Penny (1966), Bailey (1923)
[illegible] ground squirrel *[illegible]*	[illegible] snowshoe hare [illegible]	O'Donoghue (1991), Holmes (1977), Boonstra et al. (1990), Michener (1982)
[illegible]	[illegible]	Cook & Henry (1940)

TABLE 1. Continued.

Species	Prey	Source
Washington ground squirrel (*Spermophilus washingtoni*)	Conspecifics	Alcorn (1940)
South African ground squirrel (*Xerus inauris*)	Domestic fowl, other birds, turtles, other reptiles	Shortridge (1934), Ryan (1987)
African ground squirrel (*Xerus rutilus*)	Cobra	Stiles (1987)
CHIPMUNKS		
Cliff chipmunk (*Tamias dorsalis*)	Crabs	Jenkins 1989
Merriam's chipmunk (*Tamias merriami*)	Lizards, sparrows	Larson (1986)
Least chipmunk (*Tamias minimus*)	Tree swallows	Lederle et al. (1985)
Asian chipmunk (*Tamias sibiricus*)	Voles, birds, lizards, frogs	Ognev (1966)
Eastern chipmunk (*Tamias striatus*)	Conspecifics, voles, swallows, starling, snakes, frogs, salamander	Krull (1969), Seton (1929), Ginevan (1971), Hesterberg (1940), Harriot (1940), Shackleford (1966), Torres (1937)

I saw a western gray squirrel stalk a bird briefly but then retreat without completing a predation attempt. On 1 April 1993, S. B. Compton (personal communication) saw a western gray squirrel with a small, live mammal in its mouth, the size of a young *Peromyscus*, beside a road in the San Jacinto Mountains (2100 m).

Ingles (1947), Cross (1969), Jaeger (1929), and Stienecker and Browning (1970) reviewed the food habits of the western gray squirrel but reported no predation (although the latter found feather fragments in one stomach). At least six other tree squirrel species take live prey (Table 1), but the frequency of such behavior is unknown. Meat constitutes 2–11% of the diet of the eastern gray squirrel, *Sciurus carolinensis* (Packard 1956, Nixon et al. 1968); however, stomach contents analysis does not reveal how meat was obtained. Moreover, squirrels are erratic predators and not all studies are in agreement. Whereas Borell (1961) and O'Donoghue (1991) reported predation by the fox squirrel (*S. niger*) and red squirrel (*Tamiasciurus hudsonicus*), respectively, Reichard (1976) saw no predation by either species.

It is not entirely clear whether a tree squirrel attacks live prey to obtain meat per se or calcium and/or phosphorus from the bones. Shaffer and Baker (1991) noted that a fox squirrel, after killing a young blue jay, avoided the skeletal muscle and gnawed on the joints and bones near the surface of the skin. This is in agreement with other reports of tree squirrels eating bone and antlers (Cross 1969, Leach 1977). In other cases, however, sciurids have consumed specific prey organs such as the brain (Hamilton 1934, Elliott 1978) or viscera (Hesterberg 1940), or the flesh of the head (Holm 1976).

Predation by tropical tree squirrels appears to be rare. Emmons (1980) saw no predation by any of nine African species, although one *Aethosciurus* stomach contained a frog (Table 1). Glanz et al. (1982) wrote that *Sciurus granatensis* rarely eats animal foods. *Paraxerus cepapi* eats eggs, nestlings, and insects, but apparently no prey as defined here (Shortridge 1934); male *P. cepapi* sometimes kill juvenile conspecifics, but Weissenbacher (1987) regards this as a reproductive strategy rather than predation per se. Viljoen (1978) reported no predation by *Funisciurus congicus*. Small arthropods and annelids are the only known animal foods of *Sundasciurus lowii*, *Lariscus obscurus*, *Callosciurus melanogaster* (Whitten 1981), *Callosciurus erythraeus* (Setoguchi 1990), and *Tamiops mcclellandi* (Moore and Tate 1965). Borges (1990) stated that *Ratufa* is an obligate herbivore.

Th[illegible] predation in the [illegible] could be [illegible] based on the geographic distribution of observers. Certain other mammals [illegible] are facultative predators in only part of their geographic range (e.g., the chimpanzee; Curio 1976). For sciurids, the most likely explanations include the following: (1) certain tropical plants and tree barks are rich in calcium and other nutrients (see Borges 1990); (2) carnivory in the tropics may be associated with increased numbers of stomach nematodes (Emmons 1980); (3) colder climate necessitates a high fat diet; or (4) facultative predation is partly a learned behavior that can spread through a local population, but need not occur over the entire range of a species. The first hypothesis is supported by the fact that tropical tree squirrels turn to predation when caged and deprived of a normal diet (e.g., Keshava Bhat 1980).

GROUND SQUIRRELS.—Meat (live prey and carrion) is a major food source for ground squirrels worldwide, although fewer data are available regarding Old World species. Table 1 lists reports of predation by 18 species of *Spermophilus*, *Ammospermophilus*, *Marmota*, and *Xerus*. A possible exception is the Mohave ground squirrel (*Spermophilus mohavensis*), which has been studied intensively (Leitner et al. 1991) but is not known to take live vertebrate prey. The cheek pouches and stomachs of four *Sciurotamias davidianus* specimens contained only plant material (Callahan and Davis 1982), but no field data on this endemic Chinese genus are available.

FLYING SQUIRRELS.—The southern flying squirrel (*Glaucomys volans*) eats eggs, nestlings, and carrion (Bailey 1923, Landry 1970), but not consistently (Harlow and Doyle 1990). I have found no record of predation as defined here.

CHIPMUNKS.—The eastern chipmunk (*Tamias striatus*) and the Asian chipmunk (*T. sibiricus*) take a variety of prey (Table 1). Lederle et al. (1985) reported that least chipmunks (*Tamias minimus*) prey upon adult tree swallows, as well as eggs and young. Jenkins (1989) observed cliff chipmunks (*Tamias dorsalis*) in coastal Sonora, Mexico, eating crabs and other marine invertebrates in tide pools because the exact size of the [illegible] is not documented, th[illegible] borderline [illegible] predation. Larson (1986) reported that [illegible] (*Tamias merriami*) occa[illegible] and birds. The lodgepole chipmunk (*Tamias speciosus*) is somewhat specialized as an arboreal nest predator (Grinnell 1908, Grinnell and Storer 1924), but it has been reported to eat eggs rather than adult birds. Similar behavior is reported for the Uinta chipmunk (*Tamias umbrinus*) (Smith and Anderson 1982).

SIGNIFICANCE.—There are really two questions here: (1) Why eat meat? (2) Why catch it while it is still alive?

A frequent answer to the first question is that squirrels, especially reproductive females, may need a concentrated source of protein and/or certain minerals. This view is supported by studies of calcium self-selection by male and female Malabar giant squirrels (*Ratufa indica*) (Borges 1990). Smith (1968) and Carlson (1940) reported that only pregnant and lactating tree squirrels regularly eat animal food. Studies cited by Gurnell (1987) showed that female tree squirrels cannot always obtain enough calcium, phosphorus, sodium, or nitrogen from a diet of seeds. Goodrum (1940) speculated that female squirrels may need meat to reproduce successfully. Keymer and Hime (1977) reported a wild European red squirrel (*Sciurus vulgaris*) with nutritional osteodystrophy, suggesting that dietary calcium may be a limiting factor in the distribution of certain species.

A second viewpoint is that the seasonal increase in meat consumption, whether of live prey or carrion, compensates for a seasonal decline in the quality of plant food (especially protein content) and is not specifically related to reproduction. Nutrient density and water content of plants eaten by squirrels decline in spring and summer (Bintz 1984). In the Mojave Desert, plant foods evidently contain sufficient calcium, but nitrogen is likely to be limiting for desert ground squirrels that are active year-round (Karasov 1985); conversely, tree squirrels in more mesic environments have fungi available as a source of nitrogen but are more likely to need calcium seasonally (Carlson 1940, Coventry 1940, Keymer and Hime 1977). Phosphorus also may be a factor in food selection: Cano and Colome (1986) attribute the consumption of carrion by cattle in parts of South Africa to phosphorus-deficient soils. When kept on a herbivorous diet, Belding's ground squirrels select plant parts highest in protein and water (Eshelman and Jenkins 1989). Gurnell (1987) wrote that tree squirrels use animal food mainly in the summer. Weeks and Kirkpatrick

(1978) studied the "salt drive" phenomenon in fox squirrels and marmots. Clark (1968) found that the proportion of animal food in *Spermophilus richardsoni* stomachs increased from 3% in April to 24% in August. Tevis (1953) reported a similar phenomenon for chipmunks and golden-mantled squirrels.

A third hypothesis is that predation by squirrels is often incidental to killing for some other reason, usually territorial defense or reproductive competition. In other words, once the other animal is dead, it provides an energetic bonus that can be consumed without further risk. This explanation applies mainly to certain ground squirrel species (Holmes 1977, Michener 1982, Balfour 1983, Harris 1985).

The other question concerns the advantages of live prey. Carrion contains protein and other nutrients, and it does not run away or fight back. Carrion also has disadvantages: nutrient content diminishes due to desiccation and removal of organs (by the original predator or by earlier scavengers); carrion occurs in high-risk situations (near ravens, predator dens, or cars); and it may contain harmful bacteria. But the worst thing about carrion is that it may not be available when needed. Most reports of scavenging by free-living squirrels involve road kills, an artificially concentrated phenomenon.

"Quasi-prey," such as small frogs and most arthropods, are a fairly safe bet when available. Nestling birds are somewhat more difficult because of nest defense by the parents (Smith 1970, Shaffer and Baker 1991). The hardest prey to explain are adult birds, rodents, and rabbits, since these have defenses sufficient to inflict injury on a squirrel. The prevalent view is that squirrels turn to live prey only as an "emergency" food source (Reichard 1976) when other resources are depleted. This view implies that predation is a freakish event that has no real bearing on the squirrel's role in the food web. To paraphrase Landry (1970), isolated events of carnivory do not a carnivore make. (To support this statement, Landry cites an observation of a deer eating a rabbit.)

Again, however, a growing body of evidence suggests that predation is a normal component of the feeding repertoire for most sciurids, at least outside the tropics. This does not imply that squirrels are fundamental predators, but simply that they are opportunistic. One reviewer of this paper commented that squirrels are "lousy predators." Undoubtedly this is true to some extent; but neither the apparent low success rate nor the situation-specific response to potential prey is unique to squirrels. Both phenomena are reported for many obligate predators as well (Curio 1976). Moreover, Karasov (1982) found that antelope ground squirrels assimilate energy from animal foods just as efficiently as do obligate predators.

There is a learned component in predator recognition and avoidance by birds and mammals (Curio 1976, Robinson 1980). It would be a waste of energy for rabbits to avoid deer, for instance, even though one deer ate one rabbit. But if squirrels undergo dietary stress every year and begin eating peculiar things, one might expect prey to catch on. The limited evidence available suggests this is not the case. Birds apparently respond to models of squirrels near their nests (Hobson et al. 1988)—a not unexpected result, since nest predation is a frequent sciurid behavior. Smith (1970) reported that two cactus wrens (*Campylorhynchus brunneicapillus*) attacked and injured a Harris antelope squirrel (*Ammospermophilus harrisii*) near an old nest. In other contexts, however, birds and other potential prey often seem to ignore squirrels.

A clue to this blasé response may be found in the "stalking" behavior occasionally observed in tree squirrels, including the western gray squirrel as described above. This behavior is not associated with the routine operation of nest robbing but seems limited to the relatively infrequent attempts on larger prey. Klugh (1927) similarly wrote that red squirrels sometimes appear to stalk grouse or partridges, repeatedly advancing on the bird and then retreating. This is similar to my own observations of western gray squirrels reported above. The squirrel engaged in this near-caricature of a stalking predator is actually more conspicuous than usual (at least to the human observer). It is possible that the effect of obvious repeated stalking is to habituate potential prey.

Most published reports of sciurid predation are brief notes, since it is difficult to conduct a quantitative study of any rare phenomenon. However, some tentative inferences can be drawn. The proximate significance of stalking may be that the squirrel is showing conflict behavior, advancing and then retreating if the bird or other prey appears in a position to defend itself. In the ultimate sense, the squirrel should benefit from this behavior if its effect is to condition the local prey population to disregard [illegible] If most squirrels acting like predators do not follow through, then prey should learn not to respond. This behavior is analogous to the hoarding of nuts, in that the squirrel is hoarding prey confidence. Later, when normal food items are in short supply, the squirrel can exploit this conditioning. In the longer term, selection for such behavior potentially represents an entry point to a new feeding niche, particularly in marginal habitats where tree squirrels may be more likely to resort to predation.

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LATE QUATERNARY VEGETATION AND CLIMATE IN THE ESCALANTE RIVER BASIN ON THE CENTRAL COLORADO PLATEAU

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ABSTRACT.—Five alcoves (rock shelters) in the Forty-Mile Canyon–Willow Gulch area of the Escalante River Basin in southeastern Utah yielded rich deposits of late Quaternary macrobotanical remains. The deposits were sampled and the contents identified in order to construct a chronology of vegetational change. Fourteen radiocarbon dates indicate that the fossils were deposited between 12,690 and 7510 yr B.P. (years before present).

Ninety-one plant taxa were identified, 62 to species. Six species were common to all alcoves: Gambel oak (*Quercus gambelii*), box-elder (*Acer negundo*), prickly pear (*Opuntia* subgenus Platyopuntia), skunkbush (*Rhus aromatica* var. *trilobata*), serviceberry (*Amelanchier utahensis*), and Indian ricegrass (*Oryzopsis hymenoides*).

Late Pleistocene samples (>11,000 yr B.P.) contain extralocal, elevationally depressed species such as Douglas fir (*Pseudotsuga menziesii*), spruce (*Picea* sp.), and mountain mahogany (*Cercocarpus ledifolius*), and mesophytic species such as rose (*Rosa woodsii*) and water birch (*Betula occidentalis*). Early Holocene samples (11,000–8000 yr B.P.) contain no elevationally depressed conifers, and the remaining mesophytic species decrease in relative abundance. Reticulated hackberry (*Celtis reticulata*) becomes common. The terminal Early Holocene sample (8000–7000 yr B.P.) contains abundant Gambel oak and prickly pear, but little else.

Paleoclimatic interpretations for the Late Pleistocene correspond well to those of most other workers on the Colorado Plateau. Climates that were wetter and at least seasonally cooler than they are today are inferred from the macrobotanical assemblage. However, the increased moisture is attributed to higher stream base levels and increased groundwater rather than directly to increased precipitation. Early Holocene climates are interpreted as warmer and drier than those of the Late Pleistocene but still wetter than the present climate. Groundwater levels appear to be decreasing due to stream entrenchment. Terminal Early Holocene climates were much warmer and at least seasonally drier. By the end of the period, groundwater levels had decreased so much that the alcoves were unable to sustain plant communities; stream base level was probably near the present level.

Key words: Quaternary, Colorado Plateau, plants, oak, Quercus, *Pleistocene*

The Colorado Plateau has been the focus of late Quaternary paleoecologic work in the last decade; however, the late Quaternary plant communities of the central plateau, southeastern Utah, are still inadequately known because of the few case studies conducted. Late Pleistocene–Early Holocene plant communities of the central plateau have been described using macrofossils found in the alluvial deposits from Cowboy Cave (Spaulding and Peterson 1980, Spaulding and Van Devender 1980), from scattered packrat (*Neotoma* spp.) middens from the Paradox Basin (Betancourt 1984, 1990), and from the megaherbivore dung blankets from Bechan Cave (Davis et al. 1984, Mead et al. 1986), Cowboy Cave (Hansen 1980), and various alcoves (Mead and Agenbroad 1989, 1992).

The macrofossils in this study (Withers 1989) were excavated from sandstone alcove (rock shelter) alluvium and thus can represent only the community of the microhabitat where the deposit was found. The objectives of this research were to describe and to explore the paleoenvironmental implications of changes in plant communities through time.

STUDY AREA

From 1986 to 1988 field crews from Quaternary Studies Program, Northern Arizona University, explored several alcoves in the Forty-Mile Canyon and Willow Gulch areas of the Escalante River Basin (Glen Canyon National Recreation Area; Fig. 1), which is the eastern boundary of the Kaiparowits Basin. Because

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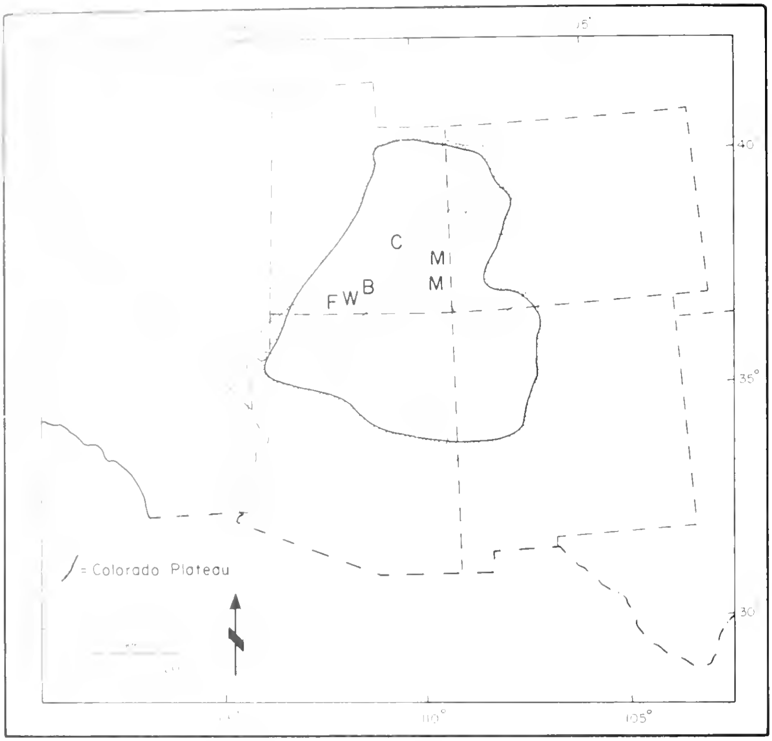


Fig. 1. Map of the Southwest locating the Colorado Plateau (delineated by stipples). F, Forty-Mile Canyon; W, Willow Gulch; B, Bechan Cave; C, Cowboy Cave; M, midden studies of Betancourt (1984, 1990).

our study is on lands administered by the National Park Service, we were requested not to locate the alcoves (on a map or in a description) with any precision. Somewhat more detailed descriptions of the alcoves are in Mead and Agenbroad (1992). Anyone needing further descriptions of locations may contact the regional scientist at the Rocky Mountain Regional Office, Denver, Colorado. At least 851 plant taxa presently live in the Kaiparowits Basin, resulting in many diverse local plant associations (Welsh et al. 1978). Taxonomic terminology follows Welsh et al. (1987).

The canyons cut through the Navajo Sandstone and the upper units of the more resistant Kayenta Formation. The alcoves appear to have been formed in the cross-bedded sandstone by spalling (wall exfoliation) facilitated by the action of moisture infiltration through joint-controlled surface drainage. All alcoves in this [illegible] appear unique [illegible] they contain [illegible] remnants of [illegible] deposits. It [illegible] that the [illegible] deposits [illegible] 13,000 years (Agenbroad and Mead manuscript). Stratified fluvial sediments are usually found on either side of steep talus slopes that are composed of sandstone blocks and boulders overlain by eolian sand. These talus slopes often contain prominent layers of macrobotanical fossils and other remains such as bones, hair, and dung. Five alcoves were chosen for study based on the abundance of plant remains evident in the deposits.

MODERN ENVIRONMENTS

Climate of the Escalante Basin is warm and semiarid with highly variable amounts of annual precipitation. Strong orographic gradients are exhibited by both temperature and precipitation. Mean annual temperature of low-elevation sites along the river is 12°C, with 250 mm or less mean annual precipitation. At high-elevation sites in the nearby Aquarius Plateau, mean annual temperature is 2°C, with 575 mm of mean annual precipitation (Webb 1985).

Vegetation in the basin ranges from Great Basin desertscrub to spruce-fir (*Picea* spp.–*Abies* spp.) forest. Low areas between 1400 m and 1700 m elevation are a mixture of shrublands and grassland (Tanner 1940). Pinyon-juniper (*Pinus* spp.–*Juniperus* spp.) woodland occurs between 1800 m and 2300 m, followed by a yellow pine-oak-manzanita (*Pinus ponderosa*–*Quercus* spp.–*Arctostaphylos pungens*) association between 2300 m and 2700 m. Above 2700 m, the southern face and top of the Aquarius Plateau support a spruce-fir forest (Webb 1985).

Topography in the immediate area of Forty-Mile Canyon and Willow Gulch is diverse. Elevation ranges from 2300 m at the top of the Kaiparowits Plateau, where the perennial streams that carve the canyons begin, to about 1100 m at the confluence of the two canyons at the Escalante River.

Pinyon-juniper woodland dominates between 2300 m and 1500 m. Below the woodland on benches and in slick-rock areas is desertscrub dominated by blackbrush (*Coleogyne ramosissima*). Within the canyons, habitats range from nearly vertical rock faces to valleylike areas; from dry, rocky slopes and creekbeds with active, steep sand dunes to riparian woodlands and hanging gardens. Valley areas are dissected by sandy washes. Many plant species such as skunkbush (*Rhus aromatica* var. *trilobata*), single-leaf ash (*Fraxinus anomala*), barberry (*Mahonia fremontii*), and serviceberry (*Amelanchier utahensis*) are found throughout the creek system in a variety of habitats, while others such as willow (*Salix* spp.), tamarisk (*Tamarix ramosissima*, introduced), box-elder (*Acer negundo*), and seep willow (*Baccaris emoryi*) are found only near permanent running water. Cottonwood (*Populus fremontii*) is common along permanent watercourses as well as areas where groundwater is near the surface.

On dry slopes above the streambed, important species include skunkbush, sagebrush (*Artemisia* spp.), blackbrush, snakeweed (*Gutierrezia* spp.), prickly pear, brickellbush (*Brickellia californica*, *B. grandiflora*), and Indian ricegrass (*Oryzopsis hymenoides*). In valleys many of these same species are common along with winter fat (*Ceratoides lanata*) and scattered individuals of Utah juniper, single-leaf ash, netleaf hackberry (*Celtis reticulata*), and cliff-rose (*Purshia mexicana*). Hackberry is widespread but uncommon, usually occurring in sheltered, shady areas.

Gambel oak (*Quercus gambelii*) is common in wet, shady areas and hanging gardens in Willow Gulch but is restricted to a relictual population in a valleylike area in the upper part of Forty-Mile Canyon. There it is found only on the shady, north-facing side of the canyon against the rocks and on the sides and bottoms of deep, sandy washes. Shrub live oak (*Q. turbinella*) is common in the upper reaches of both canyons but becomes rare as the alluvium becomes wetter. Shinnery oak (*Q. havardii*) is restricted to the driest, uppermost portions of the canyons.

In the wettest parts of the canyons, near seeps and at the edge of the creek, important species include horsetail (*Equisetum* spp.), common reed (*Phragmites australis*), sedges (*Carex* spp., *Scirpus* spp.), birchleaf buckthorn (*Rhamnus betulaefolia*), and saltgrass (*Distichlis spicata*). Box-elder is found scattered along the canyon bottom and occasionally in hanging gardens. Common hanging garden species include various ferns and mosses as well as poison ivy (*Toxicodendron rydbergii*), cardinal flower (*Lobelia cardinalis*), watercress (*Nasturtium officinale*), cardinal monkeyflower (*Mimulus cardinalis*), and columbine (*Aquilegia micrantha*).

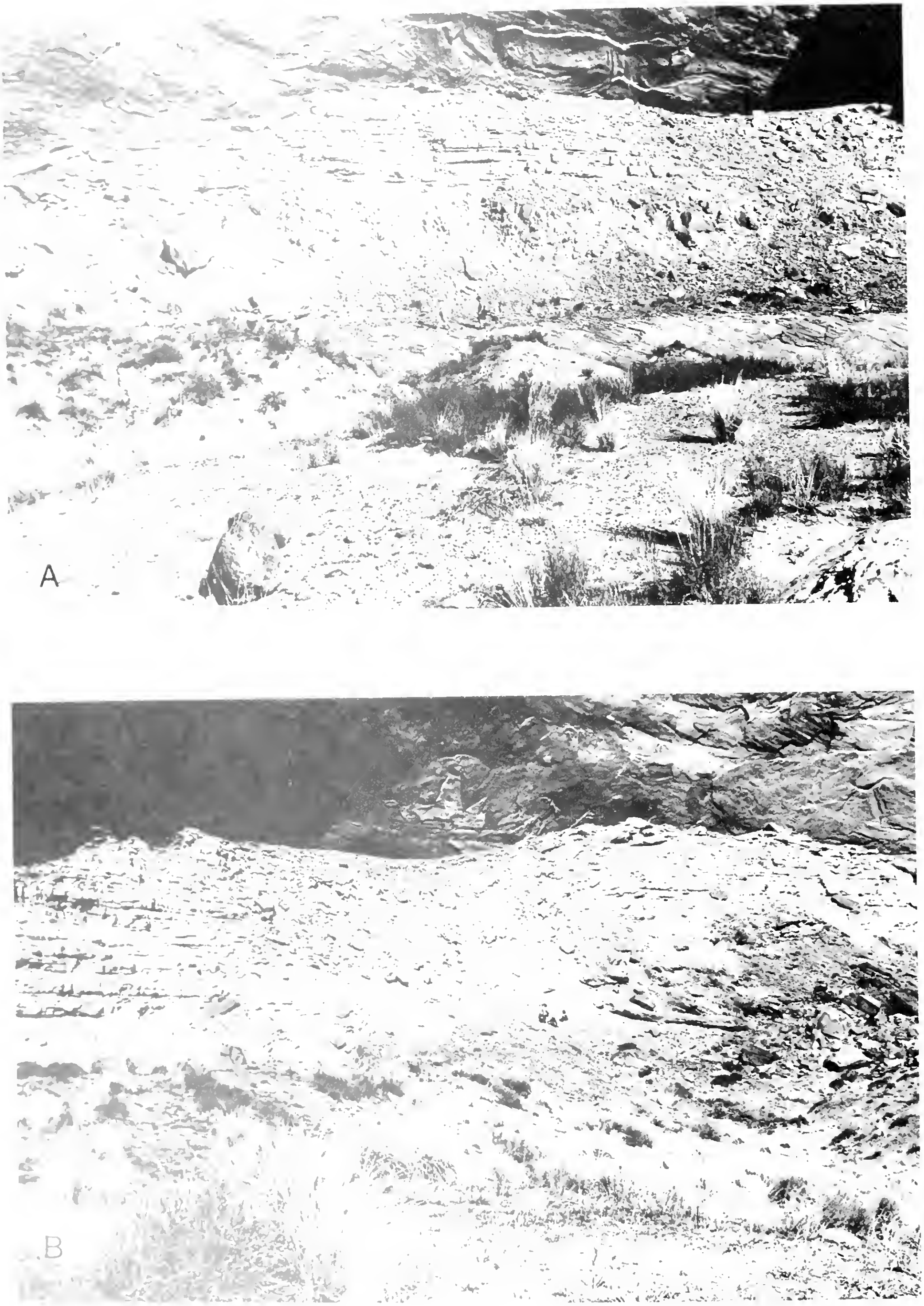
FOSSIL LOCALITIES

Hooper's Hollow, Grobot Grotto, and BF Alcove are in Forty-Mile Canyon; Shrub-Ox Alcove and Oak Haven are in Willow Gulch (Fig. 1). All are located between 1100 and 1300 m in elevation.

Forty-Mile Canyon

The alcoves in Forty-Mile Canyon are difficult to reach. Approximately 10 m of vertical or nearly vertical sandstone rises from the deeply entrenched streambed to the base of the alcoves. Streamside vegetation below BF Alcove and Grobot Grotto is dominated by willow and tamarisk, but there is little streamside vegetation below Hooper's Hollow.

Hooper's Hollow and Grobot Grotto are large (100–200 m wide), southwest-facing alcoves (Fig. 2). Tops of the deposits in both are at approximately 1200 m elevation. In both alcoves modern vegetation is characterized by desert grassland species, with a few scattered shrubs. Active and grass-stabilized sand dunes,



[illegible] of alcoves mentioned in text. A. Hooper's Hollow; B. Grobot Grotto; C. [illegible] center of B, units containing macrobotanical remains occur about [illegible] preserved botanical remains occur stratigraphically above the layered, [illegible] at all alcoves sediments are of Sangamonian age.


C


D

as well as large areas of slickrock sandstone, are also found. Indian ricegrass is the dominant species. Other species noted in the area include indigobush (*Psorothamnus fremontii*), Mormon tea (*Ephedra viridis*), snakeweed, porcupine prickly pear (*Opuntia erinacea*), buckwheat (*Eriogonum inflatum*), and dogweed (*Dyssodia pentachaeta*).

BF Alcove is relatively narrow and faces northeast (Fig. 2). It is the highest alcove in this study at about 1250 m elevation. The area just outside the alcove is a steep, grass-covered sand dune. Species present include Indian ricegrass, dropseed (*Sporobolus* sp.), and occasionally Mormon tea and snakeweed.

Willow Gulch

The alcoves in Willow Gulch are presently fairly easy to enter, usually requiring only a short climb up a steep embankment or sand dune. Shrub-Ox Alcove is located in a wide, valleylike area at 1190 m elevation and faces northwest. Gambel oak and shrub live oak grow near the stream below the alcove. Skunkbush, barberry, and brickellbush are common. Cottonwood is abundant near the creekbed and Indian ricegrass is widespread. Juniper trees are scattered across the valley. Porcupine prickly pear and hedgehog cactus (*Echinocereus* sp.) are found growing in cracks in the sandstone.

Oak Haven is the lowest alcove in this study at 1140 m elevation and faces nearly due west (Fig. 2). It is narrow and shelflike, with a fairly large, rubble-filled shelter on the north end. It is a wet, "active" alcove, although not so wet as to destroy the fossils, about 50 m above the present streambed.

This is the only alcove in which species found in fossil samples still occur alive today. Gambel oak is abundant throughout the alcove. Other arboreal species found in or near the alcove are hackberry and box-elder. Common shrubs include seep willow, sacred datura (*Datura meteloides*), serviceberry, skunkbush, roundleaf buffaloberry (*Shepherdia rotundifolia*), and [illegible]. A plunge pool is located to the south of the alcove and contains common hanging garden species.

The alcoves contain two major sedimentary [illegible] fluvial layers without organic remains [illegible] colluvial layers with fossils [illegible] sediments, of which [illegible] filled the alcoves and [illegible] some time prior to 30,000 yr B.P. They were deposited when the canyon stream was dammed downstream, possibly by either a sand dune or canyon wall collapse. At any point during deposition behind the dam, the canyon would have contained fluvial (and possibly eolian) units in the stream channel area, but there would have been lateral facies of colluvial deposition in the alcoves. Once the sediment depth had reached the threshold of the dam height, fluvial deposition would have ceased; however, lateral colluvial deposition would have continued. We are recovering fossils in the lateral colluvial facies.

When the dam was breached, sediments were probably downcut rapidly in at least the main streambed. Remaining sediments were eroded from behind and beneath by groundwater flowing between the sediments and sandstone (seeps and springs). They were also eroded by channeling and water flowing over the surface, especially at the alcove dripline. Remnants were left behind as predominantly the lateral facies in the alcoves. The oldest dated layer from our study, ca. 23,000 yr B.P. (SOA4), as well as mammoth (*Mammuthus*) dung from below the profile in Grobot Grotto, which dates ca. 26,000 yr B.P. (Mead and Agenbroad 1989), is evidence that the valley sediments had already been extensively eroded by the last full glacial (ca. 21,000 yr B.P.).

Depositional Environments and Taphonomy

The taphonomy (what happens to organic remains after death) of the localities is important to understand. Organic remains are preserved in the alcoves behind the dripline, that is, inside the shelter and away from direct effects of precipitation. Fossil remains were incorporated into the alcove sediment layers conceivably by various methods.

(1) A plant taxon could have washed into the alcove, meaning that the plant actually grew at a different location (possibly at a much higher elevation and in a different community) and was carried by stream action to a lower elevation, to finally come to deposition in one of our alcoves. Had this been the scenario, the matrix immediately around the plant remains would be fluvial in nature. The sediments would show some sort of stream action or deposition. Even the plant remains would show some sort of transport damage—which they do not show. This is not the case.

(2) A plant taxon could have been carried into the alcove by wind action. For this scenario to realistically happen, the taxon in question would have had to grow nearby enough to be carried into the alcove by wind. Long-distance transport of so many fossils is not likely given the present physiographic situation. Certainly the taxon could have lived on the land above the alcove—which is now mostly narrow slick-rock. Having any of the fossil plants recovered in the alcove actually growing above the alcove, instead of in the canyon, does not really alter our overall conclusions.

And finally, (3) a plant taxon could have been growing in or immediately outside the alcove. Plants in this scenario would have pristine macrofragments, except for situations where spalling wall rock damaged the specimens. The encasing sediments imply that only a colluvial (spalling) depositional environment is present.

It is our opinion that given the three possible depositional scenarios outlined above, the alcove and the fossils discussed here are the result of, at least predominantly, in situ deposition; that is, species actually grew inside or in the immediate vicinity of the alcove.

METHODS

Macrobotanical Fossil Collection and Analysis

Macrofossils were found in unconsolidated layers (leafmats) in the deposits or mixed with spall sands and blocks. Samples were difficult to obtain because the truncated deposits were very steep and loose (at angle of repose). Exposed surfaces were cleaned to remove loose, contaminating slumpage. The in situ leafmats were sampled by removing the mass of leaves, twigs, and other plant materials by hand or with a trowel. In between the leafmats or where plant remains were found mixed with the sand, bulk samples of sediment were collected.

Samples were taken from various locations within each site so that an accurate description of the plant community and a chronology of the site could be constructed. Generally, layers were sampled along a vertical line (profile) from the top of the deposit. At Oak Haven, Grobot Grotto, and Shrub-Ox Alcove, samples were also taken to the side of the main profile to test as much of the variability of each layer as possible. At BF Alcove, a 0.25-m pit was excavated and bulk-sampled at 10-cm intervals. These samples were dry-screened through 1-mm mesh at the site. Because the sand was so loose, it was nearly impossible to avoid mixing the layers along the edges of the pit. When sterile sand was found at 40 cm, the excavation was terminated and the pit backfilled. A similar pit was excavated at the top of the deposit (Holocene) at Grobot Grotto; however, the same slumpage problems were encountered. Since recovery was minimal, excavation was terminated at 30 cm.

In the Laboratory of Quaternary Paleontology (Northern Arizona University), bulk samples were dry-screened through a 20-mesh (0.84-mm) soil screen. They were identified by using the modern collection housed in the Museum of Northern Arizona Herbarium, consulting with various members of the biology faculty at Northern Arizona University, and examining regional literature (Gould 1951, Martin and Barkley 1961, Morris et al. 1962, Delorit 1970, Elmore 1976, Albee 1979, Welsh 1986, Welsh et al. 1987; Table 2). Plants were identified from twigs, leaves, seeds, flowers, flower parts (especially involucres), and fruits. Since the original mass and the number of unidentifiable fragments varied from sample to sample, all identified parts were counted and assigned a relative abundance according to the following scale: 1 = rare (1–2 fragments), 2 = uncommon (3–10 fragments), 3 = common (11–50 fragments), 4 = very common (51–100 fragments), 5 = abundant (>100 fragments) (following Van Devender 1973).

Radiocarbon Dating

When possible, radiocarbon dates were obtained on a single species from a single layer. In cases where no single species was abundant, a composite sample of a single species from two layers (BF Alcove) or a plant species and some fecal material from a single layer (Oak Haven) were used. Multiple dating procedures were performed in each alcove to establish a chronology. All radiocarbon dating was done by Beta Analytic Incorporated, Coral Gables, Florida (Table 1).

RESULTS

Ninety-one fossil taxa were identified, 62 to species (Withers 1989). Of those, only six were common to all alcoves: Gambel oak, box-elder, serviceberry, prickly pear, skunkbush, and Indian ricegrass. Fourteen radiocarbon dates were [illegible] in stratigraphic order for Forty-Mile Canyon and Willow Gulch samples. [illegible] BF, BF Alcove; HH, Hooper's Hollow; SOA, Shrub-Ox Alcove; OH, Oak Haven.

Sample	Radiocarbon date (yr B.P.)	Lab no.	Material dated
		Grobot Grotto	
GG0	none		—
GG1	none		—
GG2	7510 ± 160	20999	*Quercus gambelii* branch
GG3	9730 ± 170	20998	*Quercus gambelii* branch
GG4	none	—	—
GG5	9920 ± 100	20999	*Quercus gambelii* trunk
		BF Alcove	
BF1	11,790 ± 190	14727	Dung
	12,130 ± 170	20995	*Pseudotsuga menziesii* needles
		Hooper's Hollow	
HH1	10,630 ± 110	25412	*Quercus gambelii* twigs
HH2	12,010 ± 110	25411	*Quercus gambelii* twigs
		Shrub-Ox Alcove	
SOA1	8520 ± 80	25415	*Quercus gambelii* twigs
SOA2	8830 ± 190	25656	*Quercus gambelii* twigs
SOA3	12,690 ± 180	25416	*Quercus gambelii* twigs
SOA4	23,100 ± 660	25413	*Quercus* sp. limb fragment
		Oak Haven	
OH1	9180 ± 100	28929	*Quercus gambelii* branch
OH2	11,690 ± 120	25418	*Rosa woodsii* twigs
OH3	*9470 ± 150	25657	*Picea* sp. twigs and dung
OH4	none	—	—

*[illegible]

obtained to determine the age of the deposits. Materials dated included Gambel oak wood, rose (*Rosa woodsii*) branches, Douglas fir needles, spruce twigs, and dung (Table 1).

Forty-Mile Canyon

GROBOT GROTTO.—Excavation into Holocene sediments at the top of the deposit yielded few macrofossils; and since there was no obvious stratigraphy, they were treated as one sample, (GG0, not dated). This sample is identical to the modern flora as observed elsewhere in the canyon.

Four samples were collected from the 275-cm-thick Gambel oak leaf-roof spall layer that began 157 cm downslope from the datum at the top of the deposit. Three of these samples containing Gambel oak were submitted for radiocarbon dating. Twigs from the top and near the bottom of the oak leaf layer date its deposition from ca 9700 to 7500 yr B.P. (Table 1). A piece of oak stump located in situ approximately [illegible] m west [illegible] dated ca 9900 yr B.P.

Thirty-five plant taxa were identified (Table 2). Prickly pear and Gambel oak were the most abundant species in the oldest layer; blackbrush and Mormon tea were common. More species of grass (four) were identified from this sample than from any other. Indian ricegrass was common.

The remaining samples reveal no discernible change until all plant species disappeared from the alcove sometime after 7500 yr B.P. Gambel oak was the most abundant fossil species. Prickly pear was common in an undated sample from the bottom of the profile (GG4) and in the youngest sample (GG1). Other species present in small numbers include box-elder, hackberry, fishhook cactus (*Sclerocactus* sp.), Solomon's seal (*Smilacina* sp.), and Indian ricegrass. Indian ricegrass was the only species present in all samples.

BF ALCOVE.—The four samples from this alcove showed little variation except for a decrease in overall macrofossil abundance as the sterile horizon was approached. The lack of discernible stratigraphy in the test pit and low weights of any one fossil species resulted in the decision to pool the Douglas fir needles from all samples for radiocarbon dating. The two dates merge around ca. 12,000 yr. B.P. (Table 1).

Thirty-nine taxa were identified (Table 2). Most abundant were Douglas fir, bigtooth maple (*Acer grandidentatum*), box-elder, prickly pear, mountain mahogany (*Cercocarpus ledifolius*), and indigobush. Other common species included Gambel oak, currant (*Ribes* cf. *cereum*), skunkbush, hackberry, and single-leaf ash. Spruce and fir were present, represented respectively by one needle and one cone scale.

HOOPER'S HOLLOW.—The oak layer at Hooper's Hollow begins 190 cm from the datum, is up to 100 cm thick, and has been burned extensively. Two samples record plant communities of ca. 10,600 and 12,000 yr B.P. (Table 1).

Only 13 taxa were identified from this alcove, the low number reflecting the lack of preservation because of burning (Table 2). Gambel oak was very common in the Late Pleistocene sample. Uncommon or rare species identified from this sample were prickly pear, rose, box-elder, water birch (*Betula occidentalis*), spruce, and Indian ricegrass.

The Early Holocene sample records changes in the vegetation during the Pleistocene–Holocene transition. Rose, water birch, box-elder, spruce, and mountain mahogany were no longer at the site. Gambel oak and prickly pear were common. Uncommon or rare species included poison ivy, Solomon's seal, skunkbush, and Indian ricegrass.

Willow Gulch

SHRUB-OX ALCOVE.—The oak layer in Shrub-Ox Alcove began 120 cm from the datum and was about 350 cm thick. Gambel oak was dated from four samples. The oldest date (23,100 ± 660 yr B.P.) was on what appeared to be oak wood from a highly degraded part of the macrofossil layer. Only three taxa (oak, hackberry, and mountain mahogany) were recovered from this sample, but the community appears to have been similar to those of the latest Pleistocene in this and other alcoves. The remaining samples record the communities from the Late Pleistocene and the Early Holocene, ca. 12,700 to 8500 yr B.P. (Table 1).

Thirty-eight plant taxa were identified (Table 2). Gambel oak was abundant or very common in all samples. Box-elder and bigtooth maple decreased in abundance from the oldest to the youngest sample. Hackberry was common in the sample dated 8830 yr B.P. but became uncommon by 8520 yr B.P. Prickly pear was never abundant as in the other alcoves, but was only rare or uncommon in the youngest samples. An increased number of grass taxa (five) was observed in the youngest sample. Mountain mahogany was rare or uncommon in all samples. Sagebrush and saltbush were rare or uncommon in the youngest samples as were serviceberry, rose, and brickellbush.

Several species were recorded only from this alcove—willow in the Late Pleistocene sample, and Utah fendlerella (*Fendlerella utahensis*), two sedges (*Carex bella* and *Cladium californicum*), and cottonwood in the youngest sample; all were rare.

OAK HAVEN.—Oak Haven has both an oak layer and a rose layer. The stratum containing the rose layer was chosen for profiling. The deposit began 20 cm from the datum and was about 155 cm thick. The oak layer is located to the north of the profile in a pile of wall fall overlain by eolian sand.

Three samples were submitted for radiocarbon dating (Table 1). The Gambel oak sample from the oak layer dated ca. 9200 yr B.P. The two lower radiocarbon dates from the profile are reversed relative to the stratigraphy. Rose from the top of the unit dates ca. 11,700 yr B.P., while a sample of spruce twigs combined with ungulate dung from below the rose layer dates ca. 9500 yr B.P. We feel that the spruce date (Beta-25657) is equivocal, as it is a combination of two entirely different species and should not be assigned to spruce or the stratigraphic position until confirmation.

Forty taxa were identified from all samples (Table 2). The youngest sample contained abundant fossils of Gambel oak. Water birch and bigtooth maple were common. Rose is the most abundant species from the dated rose layer. Common species from the layer include Gambel oak, bigtooth maple, and Douglas fir. Rare or uncommon species include sagebrush, box-elder, water birch, prickly pear, and spruce. The two lower, undated layers contain abundant rose and spruce; water birch and box-elder were common.

The Forty-Mile Canyon–Willow Gulch Sequence

The fossil abundances of selected species from both canyons were grouped into a seriated [illegible] and Holocene deposits in BF Alcove, Grobot Grotto, Hooper's Hollow, [illegible] Utah

	[illegible]	[illegible]	GG2	GG3	GG4	BF	HH1	HH2	SOA1	SOA2	SOA3	SOA4	OH1	OH2	OH3	OH4
Graze																
[illegible]						1					–	–	–	–	–	–
[illegible]	1											–	–	–	–	–
[illegible]					1			–		–		–	–	–	–	–
[illegible]						1				–	–	–	–	–	–	–
[illegible]					1						–	–	–	–	–	–
[illegible]								–	1	–	–	–	–	–	1	–
[illegible]									1	–	–	–	–	–	–	–
[illegible]									–			–	–	–	1	–
[illegible]						1	–		–	–	–	–	1	–	–	–
[illegible]							–	–	–	–	–	–	1	–	–	–
[illegible] *Agropyron*							–	–	1	1	–	–	–	–	–	–
[illegible]									2			–	–	–	–	–
[illegible]		1					–		–	–	–	–	–	–	–	–
[illegible] *Stipa*	[illegible]	2	2	1	2	1	1	2	1	1	–	–	–	–	2	1
[illegible]							–	–		–	–	–	–	–	2	–
[illegible]										1		–		–	–	–
[illegible]						1				–		–		–	–	
[illegible]							–		1	–	–	–	–	–	–	–
[illegible]								–	1	–	–	–	–	–	–	–
[illegible] *Erioneuron*	1			–	1				–	–	–	–	–	–	–	–
Browse																
[illegible]						1		–	–	–	–	–	–	–	–	–
[illegible]						5			1	1	3	–	3	3	–	–
[illegible]			1	1	1	5	1		3	3	4	–	1	2	2	–
[illegible]				–		1					1	–	–	–	–	–
[illegible]	1					2				–	–	–	–	–	–	–
[illegible]			1						–	–	–	–	–	–	–	–
[illegible]	3	2				1		1	1	1		–	–	1	–	–
[illegible] *pungens*									–			–	–	–	1	–
[illegible]									2	1	–	–	–	2	–	–
[illegible]						1				–	–	–	–	–	–	–
[illegible] *tridentata*						1			1	1	–	–	–	–	1	–
[illegible]									–		1	–	2	2	1	–
[illegible]	1				1	1		–	1	2	–	–	–	–	–	–
[illegible]						1		–		–	–	–	–	–	–	–
[illegible]						–		–				–	–	–	1	–
[illegible]								1	1	–	–	–	3	2	1	3
[illegible]						1	–		2	1	–	–	1	1	–	–
[illegible]											–	–	–	2	2	1
[illegible]						1				–			–	–	–	–
[illegible]	1	1		1	2	3			2	3	–	1	–	–	1	–
[illegible]									1	–		–	–	–	1	–
[illegible]						3		2	2	1	1	1	1	–	2	2
[illegible]									–		–	–	–	1	–	–
[illegible]									–	–	–	–	–	–	1	–
[illegible]						2					–	–	–	–	–	–
[illegible]												–	–	–	–	–
[illegible]						2				1	–		–		–	–
[illegible]						2					–	–	–	–	–	–
[illegible]			1						–	–	–	–	–	–	–	–
[illegible]											1	–	1	–	–	–
[illegible]									–		–	–	–	–	1	–
[illegible]						2			1		–	–	–	–	1	–
[illegible]												–	–	–	1	–
[illegible]											–	–	–	–	–	–
[illegible]												–	–	–	–	–
[illegible]				1						1		–	–	–	–	–
[illegible]						1						–	–	–	–	–
[illegible]												–	–	–	–	–
[illegible]									1			–	–	–	–	–
[illegible]									1			–	1	–	–	–

TABLE 2. Continued.

	GG0	GG1	GG2	GG3	GG4	BF	HH1	HH2	SOV1	SOV2	SOV3	SOV4	OH1	OH2	OH3	OH4
Gutierrezia sp.	–	–	–			–	–								1	–
Haplopappus heterpogon	–	–		–		1	–									–
Haplopappus cf. *drummondii*	–					–					1					
Haplopappus sp.	–	–		1	–	2			1				2	1	1	–
Heterotheca sp.	–			–	–	–									1	
Hymenoxys sp.	–	–	–	–	–	1									–	–
Juniperus scopulorum	–	–	–	–	–	–	1		–						–	
Juniperus sp.	–	1	–	–	–	–	–									–
Lycium pallidum	1		–	–		–									–	
Mentzelia sp.	–	–			1	–								–		
Opuntia sp.	3	–	3		3	4	3	2	2	1				1	4	2
Phlox sp.	–			–	–	2	–	–		–	–		–	–	2	–
Picea sp.	–	–	–	–	–	1	–	1		–	–			1	5	3
Polygonum sp.			–	–	–	1	–			–						–
Populus cf. *fremontii*	–	–	–	–	–	–			1	–	–					
Pseudotsuga menziesii	–	–			–	5	–	–	–	–	–			3	1	1
Purshia tridentata	–	–	–	–	–	1	–	–	–	–		–		–	2	2
Quercus gambelii	1	3	5	5	3	3	3	4	5	4	5		5	3	2	1
Quercus sp.	–	–	–	–	–	–	–	–		–	–	1	–	–		–
Rhus aromatica var. *trilobata*	1	–	–	1	1	3	1	1	1	1	–	–	2		3	3
Ribes cf. *cereum*	–	–	–	–	–	2	–	–		–	–	–	–			–
Rosa woodsii	–	–	–	–	–	1	–	2	2	1	–	–	1	5	5	5
Salix sp.	–	–	–	–	–	–	–	–		–	1	–	–	–		–
Sclerocactus sp.	–	–	–	2	–	–	–	–			–	–	–		–	
Shepherdia rotundifolia	–	–	–	1	1	–	–	–	–	–	–		–		–	–
Smilacina sp.	–	2	2	1	–	2	2	–	–	–	–	–	–	–	1	–
Sphaeralcea sp.	–	–	–	–	–	–	–	–	1	1	–				–	–
Toxicodendron rydbergii	–	–	–	–	–	–	2	–	–	–	–	–	–	–	–	–
Trifolium sp.	1	–	–	–	–	–	–	–	–	–	–	–	–	–		
Wyethia sp.	1	–	–	–	–	1	–	–	–	–	–	–	–		–	

chronosequence (Fig. 3). Some of the variability seen in the sequence is probably an artifact of sampling and site-to-site differences rather than a real change in vegetation; however, the general trend toward decreasing abundance of mesophytic species is obvious. Douglas fir, spruce, currant, and fir do not appear in the fossil record after 11,690 yr B.P. Willow is also absent from the record after 11,690 yr B.P., but it is common in areas with permanent water in the canyons today. Rose, bigtooth maple, single-leaf ash, and mountain mahogany persist until 8520 yr B.P., while box-elder persists until 7510 yr B.P. These species were not as abundant in samples from after 11,000 yr B.P. as they were in samples prior to that time. Hackberry and water birch become more abundant in the samples after 11,000 yr B.P. Hackberry, box-elder, and single-leaf ash are found restricted to the more mesic habitats in the canyons today. Oak shows little variability in abundance throughout the sequence. The lack of deposits of any kind dating after 7510 yr B.P. suggests that the disappearance of oak from the alcoves by that time was a real event, although the species persist in other cases nearby today.

The more xerophytic species in the sequence are prickly pear, sagebrush, saltbush, skunkbush, blackbrush, and Indian ricegrass. Skunkbush persists in the record until 9180 yr B.P. and was most abundant in samples that date prior to 12,000 yr B.P. It is common and abundant in the canyons today. Prickly pear was most abundant in the sample from ca. 12,100 yr B.P. and is very common in the canyons today. Indian ricegrass, sagebrush, saltbush, and blackbrush show little variability in abundance throughout the time spanned by the record although they are not found in every sample. Today, Indian ricegrass is the most widespread species in the canyons, while the others are frequently encountered in drier habitats.

DISCUSSION

Plant communities that can be described from fossils recovered from the alcoves are much like those found in the canyons today.

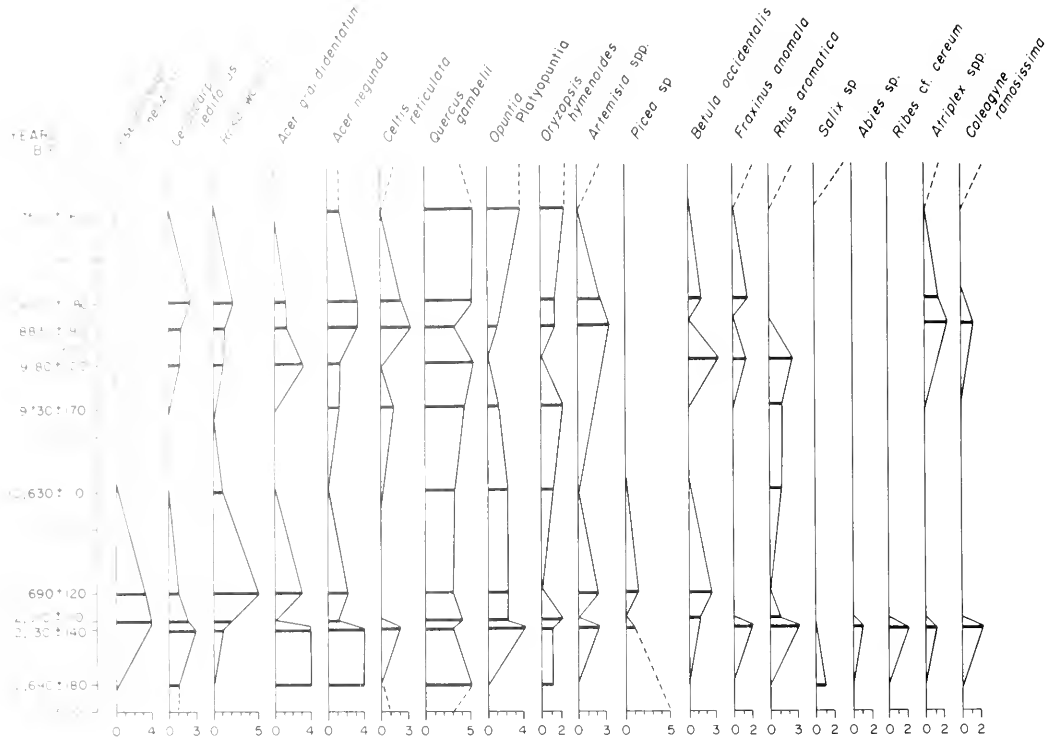


Fig. 3. Fossil abundances (rating 0 to 5) of selected plant species from all sites. See text for discussion. Dotted lines refer to inferred previous or known presence today of some species.

Major differences lie in the abundance of mesophytic, relictual species and elevationally depressed, extralocal species dating from the Late Pleistocene and Early Holocene. The most striking similarity is the abundance of Gambel oak in the fossil record and its abundance in some areas of the canyons today. While more xerophytic species such as Indian ricegrass and prickly pear have shown changes in abundance, their distributions appear to have changed little in the last 13,000 years.

Inferences regarding changing precipitation regimes based on paleovegetational changes seen in the fossil record are complicated by the [illegible] possibility that the communities were [illegible] the stream in the past than the [illegible]. Three facts suggest that the [illegible] *Bison*, camel (cf. *Camelops*), and mammoth frequented alcoves in the [illegible] ca 12,000 yr B.P. (Mead and Agenbroad [illegible]). It seems highly [illegible] would be able to gain [illegible] the stream were located in its present position since at best a steep embankment must be climbed and at worst 10 m of vertical sandstone must be scaled. (2) The existence of Oak Haven. This "active" alcove is wet and is the only alcove currently supporting Gambel oak. We believe that conditions at Oak Haven are analogous to conditions in other alcoves during the Late Pleistocene. (3) All fossil deposits are located behind the dripline, away from direct effects of precipitation, in dry section of the alcoves. This suggests that precipitation was never directly responsible for maintenance of plant communities within the alcoves but that plants were dependent on availability of groundwater flowing from seeps, springs, and the intermittent canyon stream.

Gambel oak is a definitive indicator of climate because it is sensitive to narrow limits of moisture and temperature (Grover et al. 1970, Neilson and Wullstein 1983). Its presence throughout the time spanned by this assemblage makes it suitable for making analogies, at least for temperature. It is found only in areas with mean annual temperatures of 7–10°C (Harper et al. 1985). It is indicative of at least 450 mm of annual rainfall and no less than 250 mm of winter precipitation, but its proximity to a source of groundwater such as a stream modifies these requirements (Grover et al. 1970). The extralocal species will also be used as important indicators of changing temperature and moisture regimes.

Based on the plant taxa identified from the samples (Table 2), we have designated three stages: Late Pleistocene, which includes samples dating >11,000 yr B.P. (including OH3); Early Holocene, between 11,000 and 8000 yr B.P.; and Terminal Early Holocene, between 8000 and 7000 yr B.P.

Chronology of Paleoenvironmental Change

LATE PLEISTOCENE ENVIRONMENT (>11,000 YR B.P.).—Elevationally depressed, montane species are the hallmark of Late Pleistocene plant communities. In Forty-Mile Canyon and Willow Gulch, spruce occurred as much as 900 m lower than today while water birch was up to 80 m lower. Douglas fir, currant, and mountain mahogany exhibited depressions between 260 and 300 m, and bigtooth maple was as much as 140 m lower. All these species (with the possible exception of bigtooth maple) are extralocal and probably occur no closer than the Aquarius Plateau, about 70 km to the north.

Relictual, mesophytic species were abundant during this time. Species that appear to have been common in the Late Pleistocene, such as rose and box-elder, are rare or uncommon in the canyons today. Where they do occur, they are restricted to streamside or other shady, wet situations where seasonal droughts do not occur. While Gambel oak is common is some areas of the canyons, it is also restricted to more mesic habitats. The only important xerophytic plant in the assemblages is prickly pear. The plant community of the earlier time can be interpreted as representing a somewhat cooler environment with more available moisture than is found in the alcoves today. Whether these were just seasonal differences cannot be stated at this time.

The Escalante River served as a route by which high-elevation species such as Douglas fir and spruce were able to disperse into the lower canyons. Mean annual temperature in the Aquarius Plateau today is about 2°C. However, prickly pear, which is common in the fossil samples, is rarely found in areas with mean annual temperatures below 6°C (Betancourt 1984). Gambel oak, also very common or abundant in the fossil assemblages, is found only in areas with mean annual temperatures of 7–10°C (Harper et al. 1985). Mean annual temperature in the Escalante Basin today is 10–12°C (Webb 1985). It is unlikely that cooling in the Escalante Basin during the Late Pleistocene exceeded the 3–4°C postulated by Betancourt (1984) for higher-elevation sites in the Paradox Basin. We interpret that mean annual temperature extremes in the Escalante River area may have been little different from those of today. Cold air drainage from the Aquarius Plateau and increased local water availability may have been responsible for the persistence of montane species in the canyons.

Although temperatures in the Escalante Basin may have been little different from what they are today, it is apparent that the alcoves were much wetter. We hypothesize that this was attributable to increased groundwater rather than increased local rainfall. During the Late Pleistocene these canyons contained much more valley fill than they do today, and stream base level was up to 50 m higher.

Stream entrenchment can take place during moist periods when plant cover is abundant or plentiful in the upper reaches of the stream (Antevs 1955). If rainfall was greater at higher elevations during the Late Pleistocene, as is suggested by most workers (Phillips 1977, 1984, Spaulding and Van Devender 1980, Betancourt 1984, Davis et al. 1984), then Forty-Mile and Willow creeks probably began to become entrenched during the Late Pleistocene. Because of entrenchment, the erosion of valley fill continued and groundwater levels began to decrease.

EARLY HOLOCENE ENVIRONMENT (11,000 TO 8000 YR B.P.).—The major reorganization of the plant communities during this time noted by Betancourt (1984) and other workers on the Colorado Plateau is apparent in this assemblage also. The only extralocal species found in the fossil assemblages were bigtooth maple and mountain mahogany. While still at lower elevations than they are found today, elevational depressions decreased to 30 m and 200 m, respectively. Fossils of these and other relictual, mesophytic species such as rose persisted but were less abundant than in the previous stage. Even Gambel oak decreased slightly in some of the sample. There were no apparent increases in the abundance of xerophytic plants, but decreasing abundances of mesophytic plants are evidence of changes in both temperature and moisture regimes.

Data for Forty-Mile Canyon and Willow Gulch appear to indicate two shifts in the flora that are similar to those seen in the Paradox Basin. Extralocal species except rose drop from the record prior to ca. 10,600 yr B.P. Bigtooth maple, rose, and mountain mahogany recover for a short time between ca. 10,000 and 8500 yr B.P. before dropping from the record. Gambel oak increased in abundance and hackberry became common during this time, indicating that summer moisture may have become more reliable with the establishment of the monsoonal boundary.

Shifts in the floras seen in the Escalante Basin during the Early Holocene indicate that prior to 10,600 yr B.P. temperatures or temperature extremes began to increase and moisture availability was less reliable. This resulted in decreased abundances of mesophytic plants and the upslope retreat of Douglas fir and spruce. After 10,600 yr B.P., the recovery of mesophytic species such as bigtooth maple indicated that moisture availability became more reliable again, although most species do not appear to have been as abundant as in the latest Pleistocene. This moisture is still more attributable to increased groundwater due to higher stream base level. Groundwater levels and rate of stream entrenchment fluctuated during this stage in response to fluctuating rainfall amounts as the summer monsoon moved to its present position.

A last date of ca. 8700 yr B.P. on Gambel oak leaves at Cowboy Cave is interpreted as marking the inception of a more xeric climate (Spaulding and Van Devender 1980). The sample that dates ca. 8500 yr B.P. from Shrub-Ox Alcove contains abundant Gambel oak anthers. Gambel oak on stressful xeric sites often fails to produce mature female flowers but produces an abundance of male catkins (Freeman et al. 1981). We believe the [illegible] date marks the termination of [illegible] environments in the alcoves, with the stream [illegible] more than 10 m above its present [illegible]. The alcoves were still wetter than they are [illegible] of the stage, but continued strea[illegible] culminated in drier alcove envir[illegible] end of the Early Holocene. The [illegible] became less reliable or completely dried up. Coupled with warmer seasonal temperatures, this drying resulted in the disappearance of most mesophytic species by the end of our stage.

Terminal Early Holocene environment (8000 to 7000 yr B.P.).—The one sample from this time period is from Grobot Grotto. The fact that there is only one sample in itself suggests a major change in the environment after ca. 8500 yr B.P. The sample contains only Gambel oak and prickly pear in any quantity. No plant macrofossils are found above this layer in Grobot Grotto, and none above layers dating a thousand years earlier in Shrub-Ox Alcove. This sample appears to mark the beginning of extremely dry environments in the alcoves and the establishment of the present environmental regime.

Because of its ability to reproduce vegetatively (Cottam et al. 1959), Gambel oak is able to persist in areas where seedlings are unable to become established. The stand of oaks that lived in Grobot Grotto until 7510 yr B.P. likely represents the last hold-outs before the local water table became so low that even they died. The disappearance of Gambel oak and all plants from the alcoves is interpreted as representing warmer, and at least seasonally drier, climates, and therefore the entrenching of the streambed. Stream base level was probably very near its present position by this time, leaving the alcoves high and dry, without groundwater resources to feed the seeps and springs that had previously supported the plant communities.

Biogeographic and Paleoclimatic Considerations

The Escalante River appears to have served as a major migrational route for high-elevation and mesophytic species during the Late Pleistocene. It is likely that stream base level was as much as 50 m higher than at present. At the lower elevational limits of a plant, high temperatures and deficient soil moisture produce transpiration stress in established individuals and reduce the potential for germination and seedling establishment. Relaxation of these controls can be accomplished by lowering summer temperature extremes, which would result in increased effective moisture, or by increasing precipitation (Betancourt 1984). Since drought was not a limiting factor, the elevational depression of montane species observed in this area was probably primarily the result of cooler summer temperatures, possibly facilitated by cold air drainage from the Aquarius Plateau.

Southerly displacement of the polar jet stream during the Late Pleistocene has been proposed, based on paleovegetation (Van Devender and Spaulding 1979) and modern plant distributions (Neilson and Wullstein 1983). In southeastern Utah this would result in milder, wetter winters and cooler, drier summers, an equable climate (Betancourt 1984). This interpretation corresponds well with the interpretation of the assemblages from our study as well as with those of most other workers (except Cole) on the Colorado Plateau. Gambel oak was at low-elevation sites in these canyons and at Cowboy Cave and Bechan Cave. Today, its northern limit coincides with the polar jet stream at 41° N latitude. The fossil distribution of Gambel oak suggests that the polar jet stream was displaced into the central Plateau at about 38° N latitude during the Late Pleistocene.

The terminal date for woodland communities in the Southwest is consistently younger than the traditional date of ca. 11,000 yr B.P. for the end of the Pleistocene. However, in North America this boundary is generally believed to be time-transgressive (Watson and Wright 1980) and appears to vary with latitude. Transitional communities with mesic characteristics persisted in many areas until the end of the Early Holocene, ca. 7800 yr B.P., when woodland species disappeared from modern desert areas (Van Devender 1977). The changes in vegetation during this time involved a gradual decrease in the abundance and number of woodland species and a relative increase in the importance of desert species, many of which were already present (Phillips 1977). In the eastern Grand Canyon, peak values for vegetation change (species flux) were recorded between 12,000 and 8000 yr B.P. Cole (1985) believes that Wisconsin species tended to disappear prior to the establishment of modern species. The major reorganization of vegetation zones during this time precludes the use of elevational analogs (Betancourt 1984).

In our study we postulate that warmer temperatures and increased drought stress due to fluctuating groundwater levels resulted in the upslope retreat of montane conifers and decreased abundance of mesophytic species during the Early Holocene. Mesophytic species showed a brief recovery late in our stage before disappearing from the alcoves ca. 8500 yr B.P. Sexual reproduction in oaks stopped by the end of the stage, as evidenced by the abundance of male catkins in samples from Shrub-Ox Alcove. The polar jet stream retracted to the north as the summer monsoonal boundary approached its current position. This would result in higher annual temperatures and summer extremes, less available moisture, more reliable summer precipitation, and a prolonged spring drought.

The senescence and death of oak trees and the disappearance of all vegetation from the alcoves in the canyons by ca. 7500 yr B.P. are interpreted as the result of warmer temperatures and the establishment of stream base level near its present position. Most other workers on the Colorado Plateau have interpreted their records as reflecting greater effective moisture during this time. However, our record reflects more xeric conditions as a result of decreased groundwater and possibly seasonally drier conditions. The disappearance of Gambel oak from low-elevation sites in the central Colorado Plateau may represent a northward retraction and/or upslope retreat of the species as conditions at lower elevations became too hot and dry. Conversely, the xerophytic shrub live oak, whose northern boundary currently coincides with the monsoonal boundary, and *Pinus edulis* expanded northward in response to hotter, drier conditions, similar to Antevs' Altithermal. Living populations of relict hybrids between the two oak species as well as between *P. edulis* and *P. monophylla* occur at the Middle Holocene northern limit of shrub oak and *P. edulis* and the southern limit of Gambel oak and *P. monophylla* (Lanner 1974, Neilson and Wullstein 1983). Today shrub live oak and *P. edulis* reach their northern limits far south of the relict hybrid populations.

Cole (1981) suggests that a northward shift of the summer monsoon and polar jet stream would explain his xeric record for the eastern Grand Canyon, while the same scenario is invoked to explain the occurrence of the hybrids and is consistent with a recent study of modern and fossil distributions of apomictic and sexually reproducing populations of muttongrass (*Poa fendleriana*) on the Colorado Plateau (Soreng and Van Devender 1989). It would also explain the dry record for the Escalante Basin. Those records from the central Plateau that are interpreted as wet are from higher-elevation sites where wetter, cooler situations could have persisted.

SUMMARY

The record from Forty-Mile Canyon and Willow Gulch reflects at least seasonally and/or locally wetter, more equable climates in the Late Pleistocene. The macrofossils record gradual warming and drying, which became extreme some time after 8500 yr B.P. so that all vegetation disappeared from the alcoves by 7500 yr B.P. The increased dryness is directly attributable to falling stream base levels and decreased groundwater and only indirectly to changing amounts and/or seasonality of precipitation.

Our record is in general agreement with other Colorado Plateau records except that it appears to reflect at least seasonally drier conditions during the Middle Holocene. This is probably because our sites are at lower elevations than the others. Further studies of similar macrobotanical deposits in the surrounding area, if they exist, are in order. Expansion of this record could delineate the changing position of the northern limit of Gambel oak and, by extension, the geographic positions of both the monsoon and polar jet stream throughout the late Quaternary. Additional data from this area would also help refine the geographic and temporal boundaries of both wet and dry altithermals. Additional paleobotanical studies in the area are necessary if the late Quaternary paleoecology of the central Colorado Plateau is to be adequately understood.

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BOLE VOLUME GROWTH IN STEMS OF *QUERCUS GAMBELII*

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ABSTRACT.—Shrub-form and tree-form Gambel oak (*Quercus gambelii*) stands contain a potentially significant fuelwood resource. Information on their growth characteristics can form a basis for future stand management. Stem analyses showed that height growth of shrub-form stems essentially ceased after age 50, while tree-form stems continued to increase in length until approximately age 100. Both stem forms continued to increase in basal area and volume at a relatively constant rate as the stems increased in age and size. Increases in all size measures were substantially greater in tree-form stems than in shrub-form stems. Mean bole volume for tree-form stems at age 100 was over 16 times that of shrub-form stems. Sprouts from tree-form stands would reach minimum size for fuelwood marketing in approximately 45 years.

Key words: Gambel oak, Quercus gambelii, *shrub-form, tree-form, height growth, volume growth.*

Gambel oak (*Quercus gambelii*) is a species important for wildlife habitat, watershed protection, and fuelwood. It is found in many areas of Arizona, Colorado, New Mexico, and Utah. In Utah the optimum elevations are 1700–2300 m where Gambel oak is a dominant in the Mountain Brush or mountain mahogany–oak shrub potential natural vegetation zone (Kuchler 1964, Harper et al. 1985, West 1989).

Gambel oak has a variable growth form. Normally a tall shrub or small tree, it can be found as dense, shrubby patches 1 m tall, or as widely spaced trees up to 23 m tall (Clary and Tiedemann 1986). This morphological variation prompted early taxonomists to recognize as many as eight additional species within populations now considered Gambel oak (Harper et al. 1985). The variability may have an environmental source (Neilson and Wullstein 1983), a genetic source (Pendleton et al. 1985), or both.

Sexual reproduction is sporadic, generally with limited success (Cottam et al. 1959, Neilson and Wullstein 1983, Wullstein and Neilson 1985). However, the species has a high regenerative capacity from adventitious buds situated on the lignotubers and rhizomes of existing plants (Muller 1951, Tiedemann et al. 1987). These buds give rise to numerous sprouts, particularly after fire, herbicides, woodcutting, or [illegible] the aboveground stem [illegible].

Gambel oak is particularly desirable as fuelwood because of its heat-yielding qualities—approximately 1.4 times greater than ponderosa pine (Barger and Ffolliott 1972). The superior heat-producing qualities of this species and its proximity to several major population centers have generated considerable interest in management and use of Gambel oak for fuelwood (Harper et al. 1985, Betters 1986). Retail prices reflect the heat-producing value of Gambel oak. It is typically sold for $10 more per ton than any other species (Johnson and Grosjean 1980).

Some information is available on projected growth characteristics of Gambel oak based primarily on diameter increments (Wagstaff 1984). However, no information is known to be available on the incremental growth of Gambel oak bole volumes. Because of this, we conducted this study to determine the volume growth characteristics of Gambel oak stems to assist in future management of this often ignored, but locally important, species.

METHODS

FIELD METHODS.—The plant materials for this study were collected as part of earlier studies of standing crop biomass (Clary and Tiedemann 1986, 1987). Eight small tree- and shrub-form plots were sampled within typical stands on Bald Mountain near Ephraim, Utah.

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TABLE 1. Growth curve[1] coefficients and R^2s.

Stem form	Variables		Coefficient term				
	Y	X	A	B	C	D	R^2
Shrub	Basal area	Age	814.992	.439716	.001586	355.110	0.56
Tree	Basal area	Age	330.944	.762575	.022552	56.1056	0.58
Shrub	Volume	Age	574601.	.846456	.002810	542.712	0.68
Tree	Volume	Age	169008.	.546096	.011471	76.9049	0.55
Combined	Volume	Basal area	223504	.386965	.002732	173.616	0.94
Shrub	Height	Age	4.11932	1.09578	.026754	27.2519	0.78
Tree	Height	Age	9.71913	.819354	.037815	19.0701	0.85
Shrub	Annual incr.	Volume	1363.82	.053418	.000016	3426.15	0.75
Tree	Annual incr.	Volume	2409.61	.242472	.000009	24327.8	0.80

[1] Model: $Y = A*(1 + (B - 1)*EXP(-C*(X - D)))^{(1/(1 - B))}$

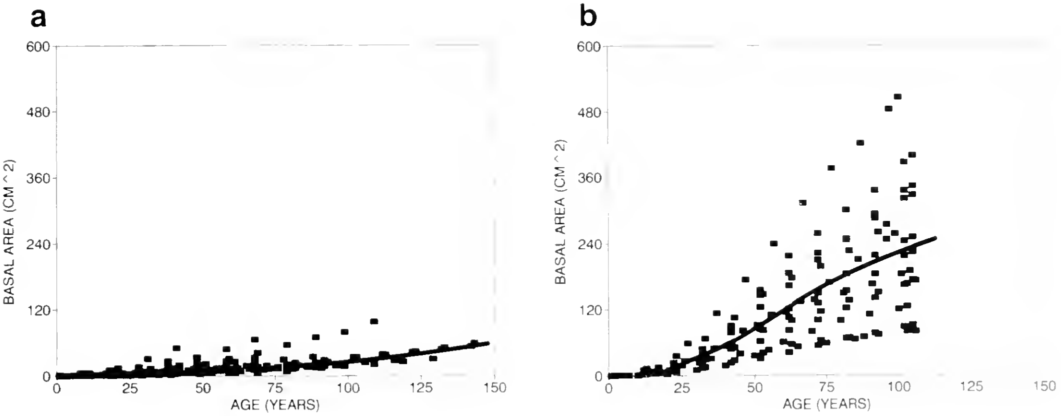

Fig. 1. Basal area (cm^2) versus age (years): a, shrub-form stems; b, tree-form stems.

These are hereafter referred to as *shrub-form*. The sample stands were on slopes of up to 40%. The plots sampled varied in size from 3 × 3 m for high densities of small stems to 9 × 9 m for plots of less dense stems. Large Gambel oak trees were represented by five stands in the Cascade Springs area of the Uinta National Forest, Utah. These are referred to as *tree-form*. Tree-form stands were visibly distinct from surrounding vegetation and occupied concave slope positions where soil depth and moisture favored tree growth. Stands had to be of sufficient size to accommodate a 100-m^2 plot. Plots were square when possible, otherwise rectangular.

Stems greater than 1 m high were counted, numbered, and measured for diameter at a height of 4 cm. Three (in tree-form plots) or five (in shrub-form plots) trees were selected at random for sampling. Stem boles were cut 4 cm above ground line and separated from branches and foliage. Where the tree bole forked, the largest fork was selected as the main bole. These boles were partitioned into 60-cm sections continuing upward until stem diameter outside-bark had decreased to approximately 1 cm. The last sections were therefore of variable length. A 10-cm length was removed from the base of each section for tree-ring analysis by the late Dr. C. Wes Ferguson and associates, Laboratory of Tree-Ring Research, University of Arizona, Tucson.

LABORATORY METHODS.—The basic approach of ring-count dating was augmented in this study by the use of dendrochronological techniques. In instances where the ring pattern was obscured or distorted, two types of controls were used to reconstruct the radial tree-ring sequence. First, a comparison was made with other areas of the cross section, with other sections from the same tree, or with other trees. The second, using

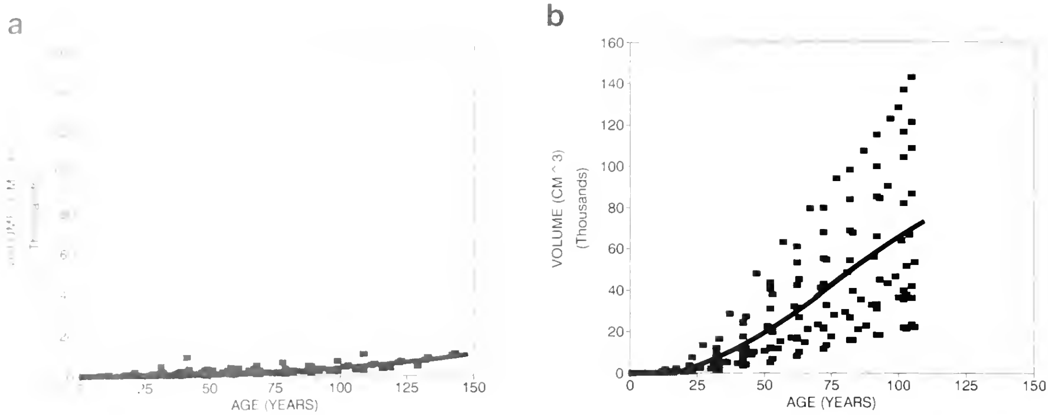

Fig. 2. Volume (cm³) versus age (years): a, shrub-form stems; b, tree-form stems.

dendrochronological principles, was to date all, or a portion thereof, of the radius in comparison with two relatively nearby established tree-ring chronologies—Nine Mile Canyon and Emory-Link. Several notable reference points were a pair of large rings at 1957 and 1958, and in some instances a wide band of vessels occurred in the 1919 ring. Some data had to be reconstructed for individual bole sections because of tree damage from fire or other injury, distortion due to whorls, etc. The diameter increments were determined to the nearest millimeter by decades, e.g., 1980–1971, progressing from the outer ring of the stem toward the pith. Partial decade growth was recorded when the beginning or ending of the section growth record fell within a decade. As the stems tended to be asymmetrical, the longest and shortest inside bark radii were recorded.

Cross-sectional area and volume calculations were made by using spreadsheet software on a personal computer. Diameter and volume values were calculated on an air-dry, inside-bark basis. The cross sectional area for a given period was determined for both ends of each section using the longest and shortest radii and assuming an elliptical shape. Section volume for each period (usually decadal) was calculated from the top and bottom cross sectional areas for the period and its section length using the parab- [illegible] (usually decadal) volumes [illegible] tions to give stem volume [illegible] heights were determined [illegible] lengths. Heights at [illegible] to the manner of [illegible] growth tips are assumed to be equally spaced throughout the section. Patterns of volume change were examined by graphic and regression methods, using periods or height segments within trees as sample units to illustrate growth trends. All regression fits were made using the Richards growth curve model (Richards 1959).

Results

Little data overlap occurred between the two populations above age 30 in the basal area versus age relationships (Figs. 1a, 1b, Table 1). At age 30 tree-form stems had mean basal area values nearly 10-fold those of shrub-form stems. Similar relationships occurred with volume versus age (Figs. 2a, 2b, Table 1). At age 100 mean stem volumes were 4049 cm^3 and 65,808 cm^3 for shrub-form and tree-form, respectively, or a difference exceeding 16-fold.

The relationship of volume to basal area was more consistent between stem forms than in the previously described relationships. A single function fit the full range of data for both populations combined (Fig. 3, Table 1).

Relationships of height to age varied between the two populations. Rates of height growth were not greatly different among populations for the first 20 years. After 50 years, however, little additional height increment occurred on shrub-form stems (Fig. 4a, Table 1). Maximum height averaged 4.1 m. Tree-form stems continued growth after age 50 at substantial, although slowly decreasing, rates until approximately 9.3 m in height was attained at age 100 (Fig. 4b, Table 1).

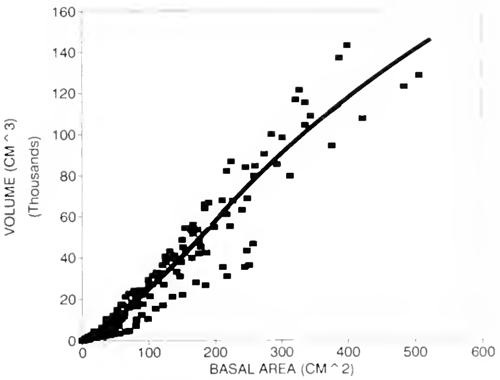

Fig. 3. Volume (cm^3) versus basal area (cm^2) for combined stem forms.

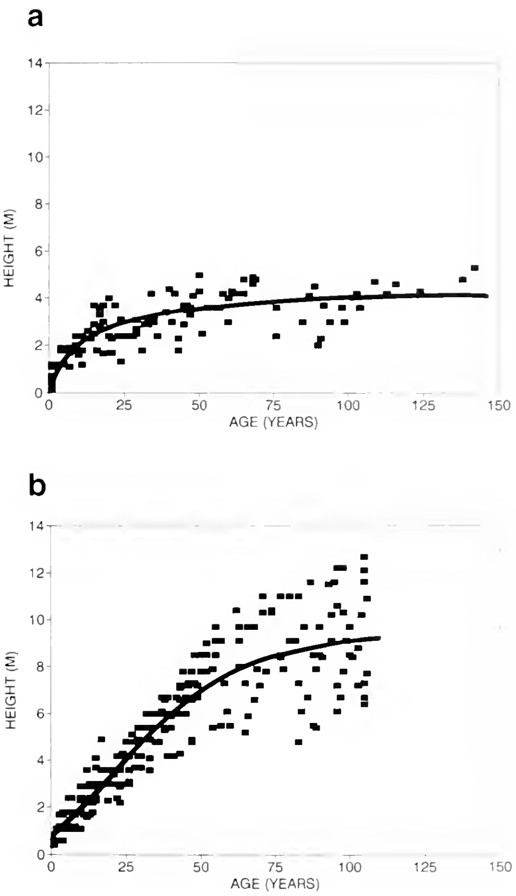

Fig. 4. Height (m) versus age (years). a, shrub-form stems; b, tree-form stems.

The relationship between annual volume increment and age was not strong for either population; R^2 values were .29–.38. A better fit was obtained between annual volume increment and total volume (R^2 = .75–.80). Annual volume increment as a function of existing volume was greater at all volumes in tree-form stems than in shrub-form stems, illustrating more vigorous growth (Figs. 5a, 5b, Table 1).

DISCUSSION

Sampling in this study was limited to central Utah, but stem sizes encountered were representative of sizes across the distribution of Gambel oak. Mean basal diameters of the stands in this study varied from 3.6–11.7 cm in shrub-form stems to 15.1–24.6 cm in tree-form stems (Clary and Tiedemann 1986, 1987). Our shrub-form stems, therefore, corresponded to the average 7.6-cm stump height diameters in western Colorado (Brown 1958). Our tree-form stems were similar in diameter to the larger stems in north central Arizona (Barger and Ffolliott 1972).

Limited information has been available concerning direct volume measures or growth characteristics of Gambel oak. A volume table based on a technique of visually estimated volume is available for Colorado (Chojnacky 1985), and one has been used in Arizona that was developed by modifying a composite volume table for trees in the Great Lakes vicinity (Barger and Ffolliott 1972). Barger and Ffolliott (1972) found that annual stand volume growth in Arizona averaged 0.24 m^3/ha, or about a 2% increment. A similar percentage increment was found in Utah for individual older trees (Wagstaff 1984). Wagstaff's (1984) data showed that diameter growth in tree-form stems slowed little in older trees; thus, the rate of basal area accumulation increased with age. In this study our estimates of annual growth in older tree-form stems were similar to those of Wagstaff, although differences in magnitude between shrub-form and tree-form stems were striking in nearly all data collected. Basal area versus age, volume versus age, height versus age, and annual volume increments in relation to total volume were different between stem forms. Volume versus basal area was the only relationship examined that appeared similar between stem forms.

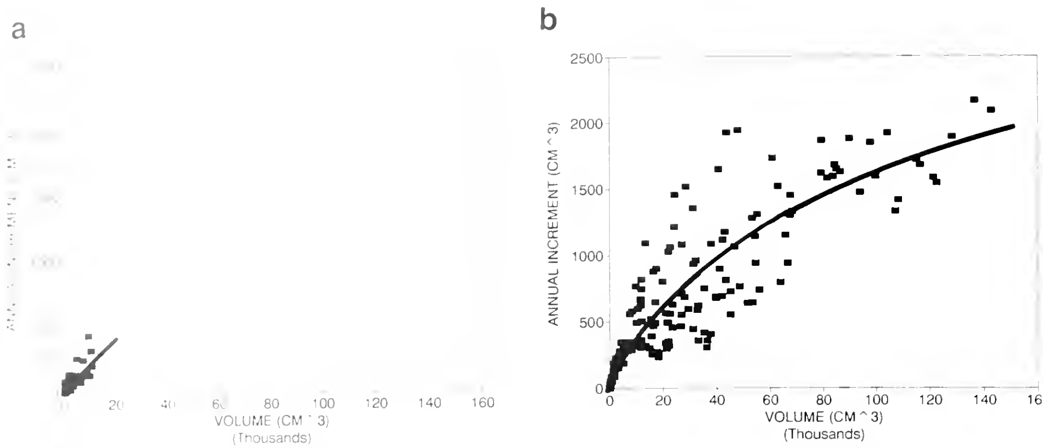

Fig. 5. Annual volume increment (cm³) versus volume (cm³): a, shrub-form stems; b, tree-form stems.

A massive underground structure, which supports rapid and normally voluminous sprouting following top removal, provides a reliable reproduction strategy that should fit well into a coppice fuelwood management cycle of harvest and regrowth (Clary and Tiedemann 1986, Tiedemann et al. 1987). This would be especially true on the more productive sites where clones of tree-form stems or larger shrub-form stems are available. While we can offer no direct evidence that tree-form stands will coppice to new tree-form stands rather than to shrub-form stands, circumstantial evidence suggests this is so. Tree-form stands in this study were separated by a distance of several kilometers; yet most of the stems of these stands were established within a 3-year period. The most likely cause would be sprouting following a widespread hot wildfire. Sprouting following such events typically results in high stem densities. As the new stand ages, a natural thinning occurs. This is reflected in old stem scars on lignotubers and rhizomes (Tiedemann et al. 1987). Scars of previous stems and the underground interconnectedness of Gambel oak clones suggest that [illegible] of stems arise repeatedly from the underground structures. These stems would [illegible] genetic makeup as the previous [illegible] growing on the same site.

[illegible] mature stands near cit[illegible] [illegible]. Maximum retail [illegible] 75,000 ha of oak clone if [illegible] sites are completely [illegible] 1984). Arizona forests have [illegible] volumes of 16 m³/ha averaged across broad clone-occupied and non-clonal areas (Barger and Ffolliott 1972). The retail value on a landscape basis, therefore, would be $740/ha (1983 dollars) if all harvestable volume were removed (Wagstaff 1984).

Gambel oak is marketable when average diameters are relatively small. Wagstaff (1984) reported that stems are salable as fuelwood when the basal diameter reaches about 9 cm (basal area of 64 cm²). This diameter, based on our stem analyses, would be attained in 45 years in our unmanaged tree-form stands. A few shrub-form stems would reach marketable size in 90 to 100 years, but a projected 170 years would be required in our average unmanaged shrub-form stands.

Our current (mature) tree-form stands with marketable volumes of 150.6–604.6 m³/ha would be worth $11,144–$44,740 per hectare of clone (Wagstaff 1984, Clary and Tiedemann 1987). Marketing of the resulting sprout growth could occur in approximately 45 years, although volumes would be much less than the original harvest. Estimated volume at age 45 would be only 25% of that attained at age 100.

Only one of our shrub-form stands had average stem diameters of marketable size, although four of the eight stands had some stems that exceeded the 9-cm-diameter requirement. The stands had mean bole volumes of 46.6–94.1 m³/ha and no apparent correlation between volume and stand density, although lower density stands tended to have larger stems. Thus, values for those stands that have attained marketable diameters could be $3448–$6963 per hectare of clone (Clary and Tiedemann 1986, Wagstaff 1984). Any estimate of marketability and value for a specific oak stand would, however, have to be determined on site.

Fuelwood sales can provide a valuable tool for oak stand management. Fuelwood cutting can generate revenue while achieving various stand modification goals, such as modifying wildlife habitat conditions (Reynolds et al. 1970) or stimulating sprouts in over-mature stands for future fuelwood production.

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AQUATIC HABITATS, LIFE HISTORY OBSERVATIONS, AND ZOOGEOGRAPHIC CONSIDERATIONS OF THE SPOTTED FROG (*RANA PRETIOSA*) IN TULE VALLEY, UTAH

Peter Hovingh[1]

ABSTRACT.— Four populations of the spotted frog, *Rana pretiosa*, occur in western Bonneville Basin. Only the Tule Valley populations occupy aquatic habitats associated with warm (28° C) and slightly saline (1700–2700 µmhos/cm) springs. The spotted frog in Tule Valley breeds in cold-water portions of the peripheral wetlands, which exhibit maximum temperature fluctuations (1–25 C), maximum conductivity up to 3200 µmhos/cm, and maximum pH values up to 9.7. Adult frogs are found in habitats with temperatures of 29° C, conductivity of 4700 µmhos/cm, and pH above 9.0 in the summer. The increased summer salinity and pH in frog habitats returns to lower values by the next breeding season due to underground recharge. Breeding in Tule Valley occurs earlier than in other Bonneville locations because of the warm-water sources. Spatial and temporal distribution of the spotted frog since the regression of Lake Bonneville 15,000 years ago and threats to present habitats are discussed.

Key words: spotted frog, Rana pretiosa, *life history, ecology, paleozoology.*

The spotted frog, *Rana pretiosa*, is an aquatic ranid occurring in northwestern North America extending southward to Nevada and Utah. In western Utah some of the sites occupied by spotted frogs were flooded by Lake Bonneville 15,000 years ago (Currey et al. 1983, Currey and Oviatt 1985). Tule Valley, one such valley flooded by Lake Bonneville, became a closed basin and separate from Lake Bonneville 14,200 years ago (Sack 1990). This valley contains numerous artesian springs on the basin floor, probably associated with faults and fractures (Stephens 1977, Wilberg and Stolp 1985). Unlike artesian springs in adjacent valleys, Tule Valley artesian springs contain neither fish nor mollusk.

The spotted frog was first noted in Tule Valley in 1980 in a study of the distribution of the spadefoot toad (Hovingh et al. 1985, Hovingh 1986). High conductivity (1000–3000 µmhos/cm) and temperatures (19–31 C) of Tule Valley artesian springs suggested special life history adaptations of the spotted frog to this habitat. This paper will describe some of the physical features of these spring systems in relation to spotted frog life history. In addition, I will postulate movements of the spotted frog in the present hydrologically closed basin during the Lake Bonneville paleolake period. Finally, I will discuss some features of Tule Valley that have contributed to the long survival of spotted frogs in this valley while the species has declined in the Wasatch Mountains of eastern Bonneville Basin in northern Utah. This report is part of a continuing aquatic survey of mollusks, leeches, and amphibians in the Great Basin.

METHODS

Tule Valley is located in western Millard and Juab counties in west central Utah (Fig. 1). Hydrologically, Tule Valley is a part of the Bonneville Basin of western Utah; as such, it has surface water impounded in saline mud flats or terminal lakes and does not drain to the ocean. The springs are located 77 km west of Delta, Utah, and occur in a north-south trend for 15 km (Figs. 1, 2) in the middle of Tule Valley. The springs consist of a source usually in bulrushes (*Scirpus americanus*), a flowing outlet in bulrushes, and a terminus (wetlands) in open ponds with or without saltgrass (*Distichlis spicata*). The springs are surrounded by greasewood (*Sarcobatus vermiculatus*) and pickleweed (*Allenrolfea occidentalis*) communities (Fautin 1946) and are similar to those described for Fish

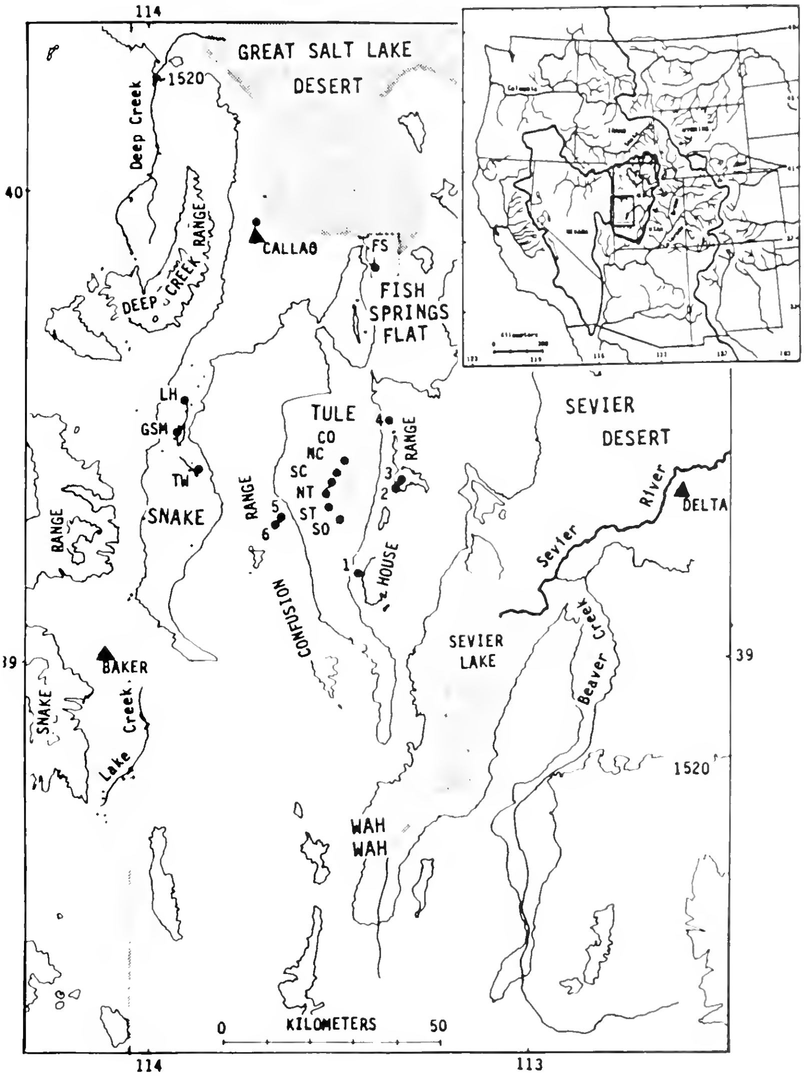


Fig. 1. Southwestern Bonneville Basin showing Tule Valley, Snake Valley, and the Sevier Desert. Within Tule Valley the basin artesian spring complexes are shown (from south to north) as South (SO), South Tule (ST), North Tule (NT), South Central (SC), North Central (NC), and Coyote (CO), as well as the mountain range springs (1–6). Spotted frogs have occurred in Snake Valley in Twin Springs (TW), Gandy Salt Marsh Springs (GSM), and Leland Harris Springs (LH) and along Deep Creek (upper left). Communities of Delta and Callao, Utah, and Baker, Nevada, are shown. Lines are contour lines representing 1520 m (5000 feet) (labeled), 2290 m, and 3050 m (10,000 feet). The inset shows the region in relation to the Bonneville Basin of Utah, eastern Nevada, and southern Idaho as well as to the Great Basin in western United States.

Springs (Bolen 1964). These springs were grouped and named in this report: (1) South Complex (5 km southeast of South Tule Springs and not shown in Figure 2); (2) South Tule Complex; (3) North Tule Complex; (4) South Central Complex (consisting of three isolated springs referred to as Willow, North Willow, and South Willow) (Stephens 1977, Wilberg and Stolp 1985, Sack 1990); (5) North Central Complex; and (6) Coyote Complex (3.5 km north of North Central Springs).

Each of the larger springs was marked distally from its source by stakes. At irregular intervals measurements of temperature, conductivity, and pH were taken at these locations. A diversity of locations was selected so that areas

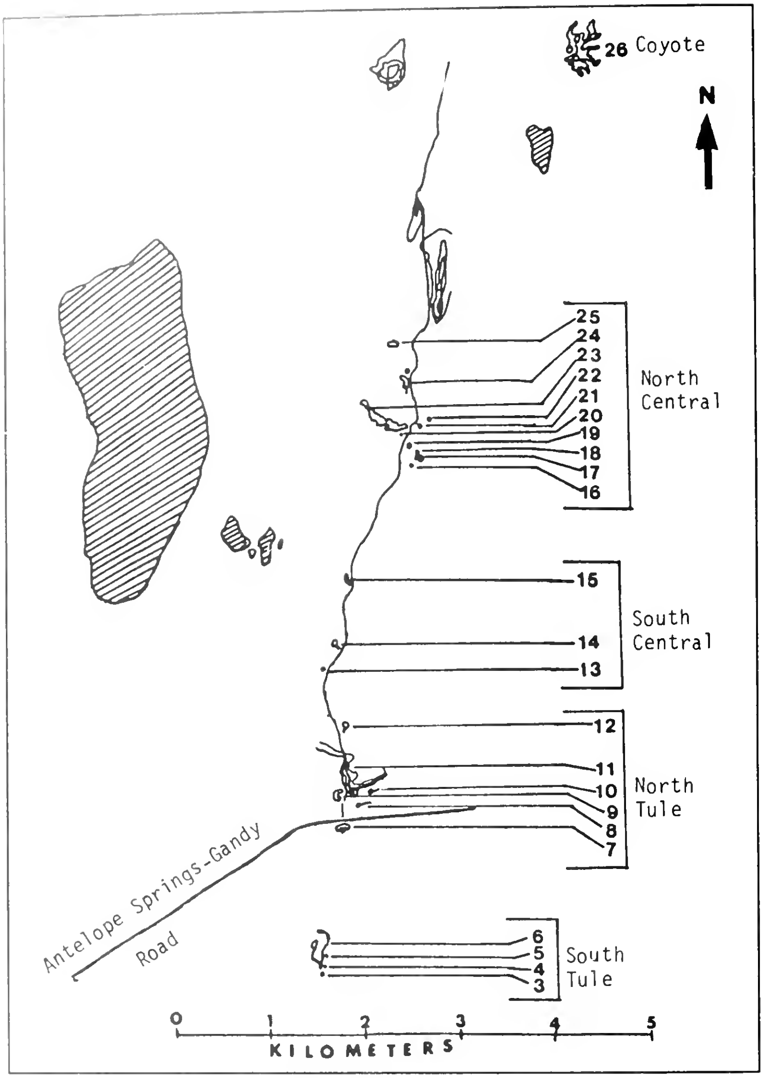


Fig. 2. Detailed map showing artesian springs in Tule Valley. The two springs in the South Complex are not shown. The [illegible] with the springs is a vehicular track that can join the Antelope Springs–Gandy road with a road to Coyote Canyon. The shaded area represents saline mud flats (not shown are the extensive saline mud flats on the east side).

of sparse and dense cover, active stream flow, and standing open waters were sampled. Conductance and temperature measurements were taken in the months of February, May, and August [illegible], whereas pH was measured in December 1981 and June 1982. Transect [illegible] in two springs to determine [illegible] variations with time of day [illegible].

Conductance [illegible] in the field using a portable [illegible] Instruments, No. 33 and [illegible]. Water samples for pH analysis were taken in the field and read within 24 h with a Beckman Model 3560 digital pH meter in the laboratory. Field pH determinations were made with the Cole-Palmer Model 5985-90 pH meter.

Complete chemical analyses such as those performed for drinking water were carried out by Utah Water Research Laboratory, Utah State University, Logan. The U.S. Geological Survey analyzed the water from North Tule Spring and Coyote Springs (Stephens 1977, Wilberg and Stolp 1985), and this investigation (5 August

1984) examined the source and two other locations in South Tule Springs.

Sizes of the springs and wetlands were estimated values obtained from tracings of aerial photographs (courtesy of the Bureau of Land Management). Tracings of the springs and control areas of known size were cut out and weighed on an electronic balance. The smaller the wetland, the less accurate are the values. The advantage of this method is that aerial photographs show irregularities of the springs in the dark due to the contrast of bulrushes against the arid carbonate soils.

Snout-vent lengths (SVL) of metamorphosed frogs and tadpoles were measured by ruler. Estimates of populations were obtained by counting egg masses in March. Egg mass numbers represent minimal breeding adult female numbers since (1) egg masses sometimes sink to the substrate and the eggs disperse and hence are not counted, (2) breeding may occur over two months and not all egg masses are counted, and (3) sometimes eggs are deposited in thick bulrushes and are not observed. Estimates of metamorphosed frog populations were attempted by individually marking frogs by toe-clipping of up to three phalanges on each of the front legs (Turner 1960). The Petersen-Lincoln estimator (White et al. 1982) of population size was utilized, but in this case the first and second samplings were not discontinuous samples and occurred over two years.

RESULTS

Distribution of Spotted Frogs in Tule Valley

Figure 2 shows the locations of artesian springs in Tule Valley, and Table 1 lists the conductivity, temperature, and area of these springs. Spotted frogs were found in South Tule Complex (#5, 6), North Tule Complex (#7, 9, 11), South Central Complex (#14, 15), and Coyote Springs Complex (#26) (see Fig. 2). During this survey spring #5 was colonized from spring #6, with the frogs traversing a distance of 4 m over carbonate soils.

The absence of spotted frogs in South Complex and North Central Complex might be explained by the high temperature of spring #1 (South Complex), the small size and distance from other inhabited springs (South Complex), or the salinity (North Central Complex). North Central Complex (#23) contains suitable habitat as indicated by its use by the spadefoot toad. *Scaphiopus intermontanus*, which breeds in distal reaches of this spring (Hovingh et al. 1985). The absence of ranids in this spring suggests a paleozoological explanation. Prior to the increased spring flows from the high precipitation years of 1980–84, first expressed in 1983, North Central Complex contained the only stands of *Typha domingensis* (#23) and *Scirpus acutus* (#19) in Tule Valley, suggesting a different aquatic habitat or history.

Coyote Complex #26, consisting of four springs feeding a common wetland, is the largest spring in Tule Valley. This amoeboid-shaped spring had an outside perimeter of 5 km in 1981. The spring sources contained a higher conductivity than other springs with spotted frogs (2700 versus 1800 µmhos), and during the summer this conductivity in distal reaches of the spring had values of 1900–6600 µmhos, with the higher values occurring in standing open waters (Table 1). Adult frogs were observed on 22 May, 19 June, 8 August, and 19 September in areas that had a temperature range of 17–29°C and a conductivity range of 2000–4700 µmhos (5000 µmhos approximates 0.25% salinity). Egg masses were found in areas with a temperature range of 10–14°C and conductivity range of 2500–3600 µmhos on 7 March. Figure 3 shows ranges of temperature and conductivity throughout the year at South Tule Complex #6; temperature distal to the source was less than the source, whereas conductivity was higher and lower than the source in these same locations.

The increase in conductivity in summer in standing open waters and the subsequent decrease in autumn and winter suggest that evaporation of the waters contributes to this increase. The decrease of conductivity in autumn and winter from the summer values suggests that water repercolates into subsurface flows. Water repercolation into subsurface flows was highly visible in springs #6, 7, 9, 11, and 15, where water poured into a hole that resulted from the weight of cattle hooves on the aquatic habitat. One hole measured 60 cm deep. The natural slow recharge of water into the soils contributes to the maintenance of more or less constant conductivity values in these distal reaches through the years.

Since conductivity increased in standing open water, pH measurements were made; these values increased from 7.5 (spring source) to 9.5 in the distal reaches of South Tule Complex (#6) in the summer (Fig. 4). Spotted frogs

Table 1. [illegible] Tule Valley artesian springs.

Spring	[illegible]	Temp. (°C)	Conductivity (µmhos)	Temperature range (°C) Dec 3	Aug 8	Conductivity range (µmhos)	Surface area (m²)
[illegible]							
#1	2	1	1900	12–32	18–32	1800–2300	nd*
[illegible]		2–29	1200–5300				nd*
South Tule Complex							
#3		2–26	2400–4000				50
#4		11–24	1700–2100				70
#5		17–27	1100–2100				600
#6	14	28	1800	2–29	19–29	1300–3000	19000
North Tule Complex							
#7	10	27	1800	0–28	16–28	1100–4000	4700
#8		28	1700				500
#9	8	25–27	1700–1800	0–27	24–30	1100–2800	7800
#10	2	25	1700	18–26	27–28	1400–2200	1500
#11	7	28	1800	7–28	25–30	1600–2100	11000
#12	3	22	1800	0–22	23–26	1100–2500	4800
South Central Complex (Willow Springs)							
#13		23–28	1400–2000				1400
#14	4	26	1900	3–26	22–27	1100–2300	3100
#15	5	11	1700	2–11	24–28	1600–2500	4700
North Central Complex							
#16	2	2–27	1500–4300				4500
#17		3–26	8700–16000				nd*
#18		1–19	3700–7600				500
#19		3–31	19000–81000				nd*
#20		7–23	1800–2800				1000
#21		5–23	39000–61000				nd*
#22		4–30	3000–6100				400
#23	7	16–29	1900–4100	3–16	24–34	1700–5300	49000
#24	3	3–30	1200–6800	3–9	21–26		7100
#25	2	7–22	1900–9200				5200
Coyote Complex							
#26	52	28	2700	0–28	20–31	1900–6600	97000

[illegible]

[illegible] of sites sampled at the spring complex. The range of temperature and conductivity in these cases represents the extremes [illegible] at each sample site in 1981. Spring #9 had two sources flowing into a common pool, and spring #26 had four sources flowing [illegible]

occupied these distal reaches in summer and egg masses were found here in spring. Water analyses at South Tule Complex (#6) at the source, after the water flowed through bulrushes (Site L, Fig. 1), and in standing open water (Site M, Fig. 1) showed a decline in calcium and bicarbonate in the standing open water (Table 2). A slight decline in sodium and sulfate compared to the source occurred after the flow passed the bulrushes. Table 2 shows [illegible] results and compares these values of [illegible] Complex (#6) with previously published [illegible] Tule and Coyote complexes. Of note is the observation that Coyote Complex contains more sodium and chloride than South Tule and North Tule complexes.

Water originating from Coyote Complex #26 contained over 1400 mg/L dissolved solids (Stephens 1977). In the summer conductivity doubled in some portions of the wetlands, suggesting that dissolved solids increase in these areas (Fig. 3). It is unknown whether spotted frogs avoid areas with high dissolved solids, but refugia do occur within the springs that actually have less conductivity than the spring sources (Fig. 3). Frogs can likewise move to areas with

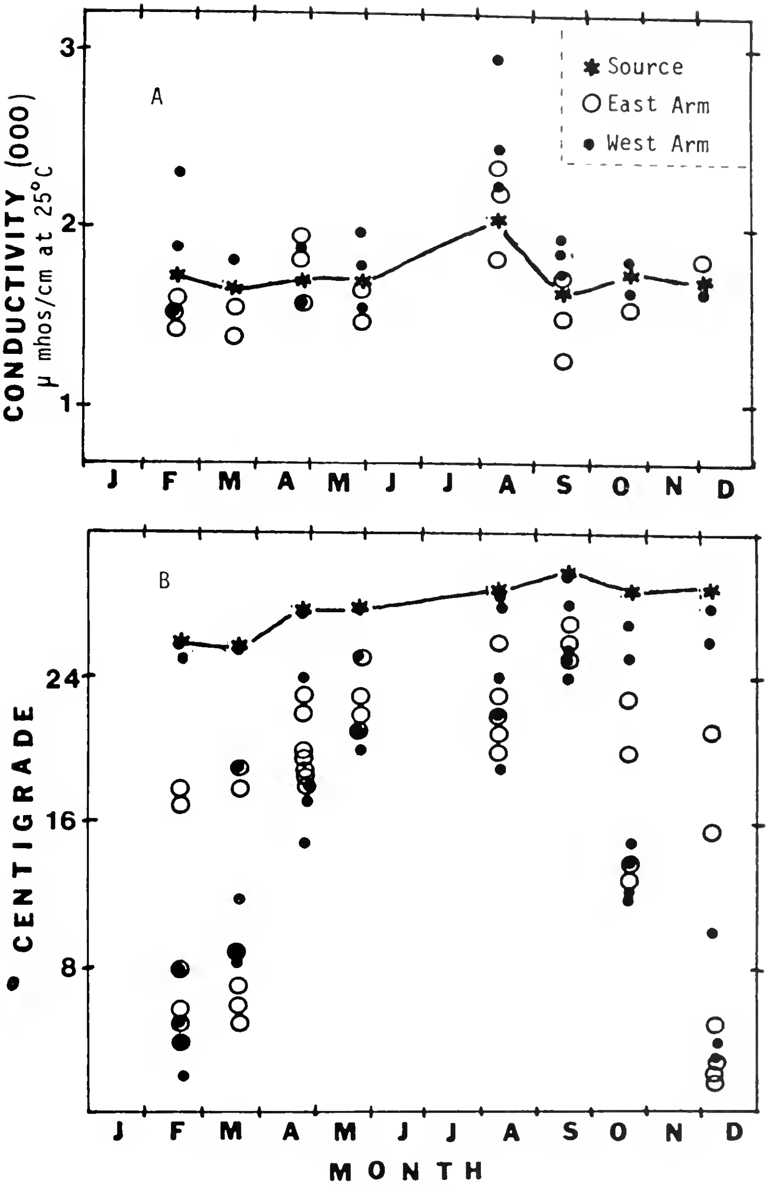
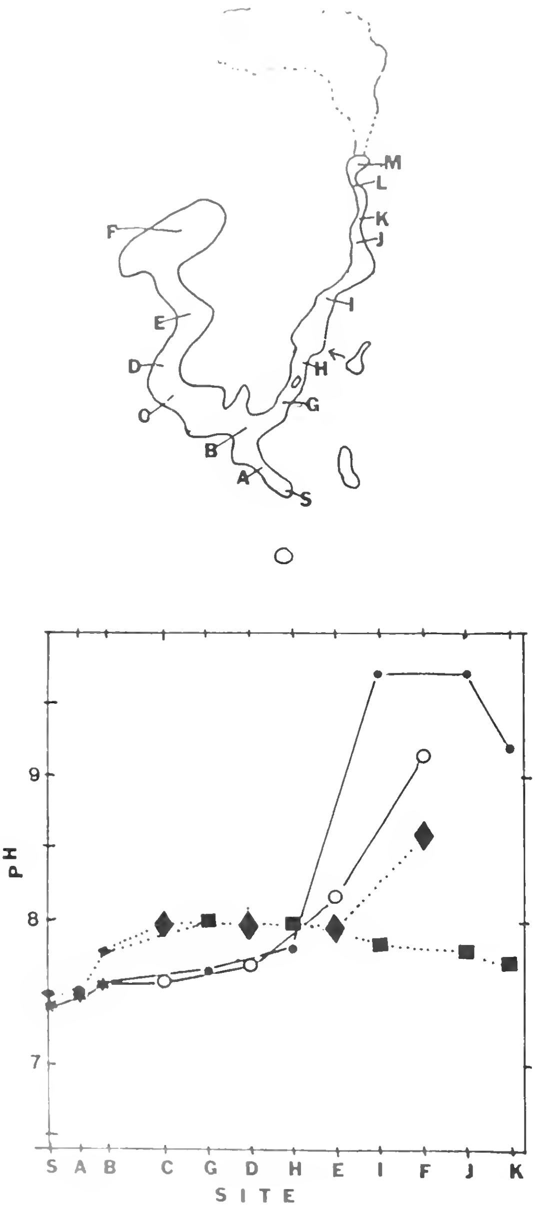


Fig. 3. Conductivity (μmhos/cm corrected to 25°C) (A, upper figure) and temperature (°C) (B, lower figure) with time of year at South Tule Complex #6. A line connects the measurements of the source. Data represent measurements taken at sites shown in Figure 4.

lower pH, but it appears that they tolerate pH of 9.5 as indicated by the presence of adults in such habitats.

As a response to the wet years of 1980–84, flows of the springs increased in 1983 and were still expanded in 1990. Many springs in the North Central Complex coalesced; North Tule #9 flowed into North Tule #11, North Tule #11 flowed into a previously dry east arm, and South Tule #5 flowed into South Tule #6. Besides these increases in flows, *Typha domingensis* became established in areas previously occupied by greasewood, and *Typha latifolia* became established in Coyote Complex. Although spotted frogs now bred in arms of Coyote Springs that previously were uninhabited by frogs, they did



[illegible] of South Tule Complex showing [illegible] upper figure. The source is [illegible] line. Distal to M represents the [illegible] years cattails grow [illegible]. No measurements [illegible] shows the pH measurements [illegible] dotted lines, winter [illegible] squares, east arm in winter [illegible] and solid circles, east arm in [illegible]

not inhabit the cattails of South Tule Spring #6. Spotted frogs moved from the south arm of North Tule #11 (greatly reduced by an outflow into a hole) to the newly flooded east arm.

Spotted Frog Life History Observations

The spotted frog is described as inhabiting cold, permanent waters or the peripheral shallow waters, which often have large daily temperature fluctuations in British Columbia (Licht 1969) and Wyoming (Turner 1960, Turner and Dumas 1972). Tule Valley is one of the southernmost localities inhabited by the spotted frog and has habitats more saline than normal. Temperatures at the water sources are higher than those at which spotted frogs initiate movement to other sites (26°C) (Turner 1960) and are at the lethal range for larval development (28°C) (Licht 1971).

The frog is found in distal portions of the springs in Tule Valley where temperature, conductivity, and pH show the greatest variation. Breeding occurs in open, shallow pools of water surrounded by bulrushes in these distal reaches or in the cattle-impacted region between the arid land and bulrushes. In South Tule Complex #6 frogs bred from B to F (west arm) and H to J (east arm) (see Fig. 4). In the summer adults occurred at the edges of wetlands in places where they were protected by bulrushes upon disturbance. No breeding occurred in the cattail-dominated areas that were formed as a result of the 1980–84 wet cycle.

Table 3 summarizes the life history of the spotted frog in Tule Valley. Adults emerge in early March or, if the season is warm, in late February. Males emerge before females as indicated at South Central Complex (#15), where 24 frogs, all males, were captured on 2 March 1990. At this time no egg masses were found. Emergence in South Central Complex (#15) was later than in other springs. On 12 March 1988, when no frogs or egg masses were seen at #15, egg masses and hatchlings were observed in South Tule Complex (#6). This delay could be a result of the lower spring source temperature of 11°C at #15 versus the higher temperatures of 28°C at other springs. On 13 March 1988 Gandy Salt Marsh Springs and Twin Springs (see Fig. 1 for locations) in adjacent Snake Valley were still under ice, again suggesting the warm spring sources in Tule Valley accelerate the breeding

TABLE 2. Major ion analysis of water in selected springs in Tule Valley.

	North Tule Springs		Coyote Springs			South Tule Springs wetlands		
	(1)	(2)	(1)	(2)	(2)	Source	Site I	Site M
Year analyzed	1974	1983	1974	1981	1983	1984	1984	1984
Specific conductance (µmhos/cm)	1590	1620	2400	2380	2500	1700	1590	1430
Total dissolved solids (mg/L)	992	910	1430	1450	1460	910	930	880
pH		7.7	–	7.3	8.2	7.7	7.6	9.3
Calcium (mMolar)	1.80	1.73	1.78	1.80	1.78	1.46	1.44	0.92
Magnesium (mMolar)	1.69	1.44	1.56	1.73	1.69	1.24	1.29	1.24
Sodium (mMolar)	8.74	8.70	15.2	16.2	16.5	8.93	8.78	8.78
Potassium (mMolar)	0.51	0.46	0.95	0.77	0.87	0.45	0.49	0.49
Bicarbonate (mMolar)	4.07	–	4.36			4.51	4.46	2.56
Sulfate (mMolar)	2.73	2.50	3.44	3.23	3.54	2.36	2.14	2.16
Chloride (mMolar)	6.48	6.76	12.7	13.0	13.2	6.48	6.59	6.59

1 Data from Stevens (1977)
2 Data from Wilberg and Stolp (1985)

season. Eggs were laid under conditions in which water freezes at night, once entrapping breeding males in the ice (21 March 1982). Breeding can be interrupted by a recurrence of cold weather as suggested by observations on 27 March 1983 and 23 March 1985, when breeding frogs and tadpoles were concurrently observed. Egg deposition and chorusing frogs occurred until early April at #15 (4 April 1981). Although only minor fluctuations of temperature (2–3°C) occurred at a given location throughout the day where the source current flowed in March, the temperature could fluctuate at least 8 C during the day in the peripheral locations where breeding occurred. Eggs were observed to hatch in late March and early April, and tadpoles (SVL, 12 mm) were observed until early May in 1981, after which no tadpoles were found. After breeding, adults could not be observed until the end of May as indicated by the observation of 5 adults between the third week in April and the third week in May, and 139 adults between the fourth week of May and the third week of June. Young-of-the-year (length less than 40 mm SVL based on the observation that breeding adults were larger than 40 mm) were found from mid-June to late September. One juvenile observed on 2 May 1987 possibly metamorphosed the previous year. Adults were seen until the end of September.

Spotted frogs typically avoided the warm waters of the springs. Two adult frogs were seen in waters with temperature of 28° C. The breeding habitat at North Tule Complex (#11) in March had temperatures that varied from 1–8 C in early morning to 7–12 C in late afternoon. Temperatures ranged from 1–3 C in early morning to 4–7 C in late afternoon in South Central Complex #15 under breeding conditions. This compares with breeding temperatures of 6°C in British Columbia (Licht 1969) and 14 C in Provo, Utah (Morris and Tanner 1969). By June, temperatures in #11 and #15 in these same locations varied from 14–18 C in early morning to 19–23 C in late afternoon. Temperatures remained below lethal levels to developing tadpoles as determined by Licht (1971) and Turner (1960).

Adult breeding size (measured during the breeding season) ranged from 43 to 66 mm for females (N = 179), with the largest size class being 55 mm, and from 40 to 59 mm for males (N = 105), with the largest size class being 45 mm. Female size in Tule Valley is 5 mm smaller, and maximum adult sizes are also smaller than at other locations (Turner 1960, Morris and Tanner 1969, Turner and Dumas 1972, Licht 1975).

Several studies have marked spotted frogs to determine population numbers, growth rates, and movement (Turner 1960, Carpenter 1954). At South Central Complex (#15), 31 adult frogs were marked, and one frog was recovered in the subsequent year after 99 had been examined. The percent recovery of frogs was 3%, compared to 40% (from a total of 54 marked) in Jackson Hole, Wyoming, in a single season (Carpenter 1954) and 27% (from a total of 1433 marked in a four-year study) in Yellowstone (Turner 1960). Use of the Pederson-Lincoln

TABLE 3. Seasonal activity of spotted frog in Tule Valley.

Month	February				March				April				May				June				July				August				September			
Week	1	2	3	4	1	2	3	4	1	2	3	4	1	2	3	4	1	2	3	4	1	2	3	4	1	2	3	4	1	2	3	4
Adults[a]								+	+		+	+	+		+	+	+	+	+			+			+						+	+
Mating adults				+			+	+	+																							
Fresh eggs									+		+																					
Embryonic eggs							+	+	+		+																					
Tadpoles							+	+	+		+	+																				
Immature[b]													+						+						+					+		

[a]Adults were seen in April and May with 5 adults seen from the third week in April to the third week in May as compared to 139 frogs seen from the fourth week of May to the third week of June.
[b]Immature frogs were identified as having a snout-vent length less than 40 mm (based on the observation that the SVL of breeding frogs was greater than 40 mm).

index yielded an estimate of some 3000 frogs at Spring #15. However, this estimate is speculative since only one frog was recovered. It would be necessary to mark many more frogs for population estimates to be reliable. This one marked female frog measured 44 mm on 8 March 1981 and 53 mm on 12 June 1982, and thus grew 9 mm in 15 months. This is comparable to growth rates reported by Licht (1975) and much faster than those reported by Turner (1960); it may reflect warmer climatic conditions and longer growing season.

Population numbers can be estimated by egg mass counts (Table 4). These counts reflect the breeding population, with each egg mass representing a minimum of one female. Of note here is the tally for South Central Complex (#14). This spring contains a small population of spotted frogs. In 1981 there were 33 egg masses; in 1982, 2 egg masses; and in 1991, 11 egg masses (Table 4). South Central Complex #14 contains a sustainable population. Egg mass numbers suggest the largest populations of spotted frogs occur in Coyote Complex (#26), South Central Complex (#15), and South Tule Complex (#6).

Direct movements of spotted frogs in Yellowstone extended up to 1290 m in 92 days and 700 m in 2 days (Turner 1960). In Jackson Hole the maximum total direct distance was 723 m over 24 days with some movements of 13 m per day (Carpenter 1954). In Tule Valley the movements were confined to areas within springs and wetlands as the land between springs consists of open spaces of carbonate soils among greasewood. In one year one movement occurred from Spring #6 to Spring #5 for breeding, a distance of about 1 km over carbonate soils. Movements could possibly occur during the wet months of April and May, but adults were not seen at that time. Movement could only happen within the North Tule Complex in a wet cycle like that occurring in 1980–84, a cycle that occurred only once historically between 1865 and 1880 (Gwynn 1989).

Predation upon Spotted Frogs

Two aquatic insect larvae were observed on egg masses: predaceous diving beetle (Dytiscidae) and crane fly (Tipulidae). One other aquatic insect, *Belostoma bakerii* (Belostomatidae, giant water bug), was found in the spring source as well as the peripheral habitats and has a potential for preying on tadpoles. The leech *Haemopis marmorata* was also observed on egg masses, and another leech, *Erpobdella punctata*, has the potential of devouring tadpoles. Occasionally, partially devoured spotted frogs were observed. In one case three regurgitated and partially devoured spotted frogs on land, one dead undevoured frog in the water, and one live frog several meters on land were observed. This observation suggested predation by a coyote, *Canis latrans*. Birds such as grebes (Podicipedidae), herons (Ardeidae), and ibises (Threskiornithidae) were rare in these aquatic habitats; Mallards (*Anas platyrhynchos*), Cinnamon Teals (*Anas cyanoptera*), and American Coots (*Fulica americana*) were common (Hovingh 1992). Predation on spotted frogs by these waterfowl is unknown in Tule Valley. Northern Harrier (*Circus cyaneus*) and Common Ravens (*Corvus corax*) are both common and potential predators.

DISCUSSION

Habitats of the spotted frog in Tule Valley include the cold-water portion of thermal springs. This habitat contrasts with those in British Columbia where spotted frogs occupy

TABLE 4. Egg mass census of spotted frogs in Tule Valley.

Date	Numbers of egg masses						
	Coyote #26	North Willow #15	Willow #14	North Tule Complex #11	#10	#7	South Tule #6
7 March 1981	278	59+	0	67	62	0	139
21 March 1981	+[a]	–	33				
21 March 1982	–[b]	+	2	+	+	40	
23 March 1985	–	+	0	+	+	5	
2 March 1990	462	+	–	5	0	0	32
15 March 1991	–	+	11	13	46	26	

[a] Additional egg masses that could not be quantified

[b] Did not survey

shallow, warm-water regions of cold streams (Licht 1971). In distal reaches of the spring source in Tule Valley, conductivity, pH, and temperature show the greatest variations; in British Columbia, habitat showed the greatest temperature variations. Thus, the spotted frog utilizes habitats with widely varying physical and chemical parameters.

A unique feature of Tule Valley aquatic habitats is the high summer values of conductivity and pH that decline to pre-summer levels in the autumn and winter. This "water purification" can be attributed to another unique feature of these artesian springs. Much of the flow from the springs is absorbed into the ground (ground water recharge) and probably surfaces via seepage springs at the lateral edges of saline mud flats on each side of the artesian springs. Artesian springs are on a small ridge 3–8 m above these saline mud flats; this elevational difference allows the subsurface flows. Seepage springs adjacent to saline mud flats have high conductivity, suggesting that groundwater supplying these springs follows an underground saline layer that underlies the central basin. It is in this morphology that cattle hooves can puncture holes in many of the wetlands and thus cause water to pour as miniature waterfalls back into the ground. Thus, these Tule Valley springs have a unique morphology that has allowed the spotted frog to survive for some 13,000 years in a saline environment and to utilize the distal portions of the springs without an increase in salinity. The adjacent Snake Valley springs are a contrast to the Tule Valley springs in that the low-conductivity outflows to the wetlands drain into the Gandy Salt Marsh pond, thus maintaining more constant conductivity and pH.

Presently, Tule Valley spotted frog habitats are very isolated from each other as the dry carbonate soils do not allow movement among springs. The exception is in South Tule complex, where spotted frogs moved from #6 to the unoccupied #5 and now breed therein. The wet cycle of 1980–84 coalesced two springs in North Tule complex (#9 flowed into #11) that could allow an exchange of frogs. Historically, the wet cycle has occurred twice: 1980–84 and 1865–80. In both periods the Great Salt Lake reached an elevation of 1284 m (Gwynn 1989). During the Holocene the Great Salt Lake reached an elevation of 1287 m (Currey 1990); but it is unknown whether this wet cycle allowed spotted frog movement among the springs. The wet cycles that caused the formation of Gilbert shoreline (elevation 1295 m, 10,900–10,300 years ago) (Currey 1990) and the Lake Gunnison (Sevier basin) drainage into the Great Salt Lake desert via the Old River Bed (13,000–11,000 years ago) (Oviatt 1988) may have affected distribution of the spotted frog within Tule Valley aquatic habitats. Both North Tule #11 and South Tule #6 have extended dry outlets that once drained these springs to saline mud flats west of the springs.

Since aquatic habitats in Tule Valley were under extensive amounts of water during the Lake Bonneville times 15,000 years ago, the spotted frog had to emigrate to these "new" habitats on the valley floor. Such an emigration occurred in Tule Valley springs during regressive stages of Lake Bonneville 14,500 years ago; both fish and mollusk were exterminated during this time. Three models are suggested to explain the presence of spotted frogs in Tule Valllley. (1) Spotted frogs were always in Tule Valley, and as the lake rose, these spotted frogs could always [illegible] of the basin. (2) Spotted frogs could have migrated from adjacent Snake Valley during high-water times; in Snake Valley the frogs occupied habitats above the highest shoreline. This would suggest the presence of spotted frogs in Lake Creek drainage (see Fig. 1) in southern Snake Valley. However, there are no frogs in southern Snake Valley today, and spotted frogs now occupy habitats in Snake Valley that were flooded by Lake Bonneville. (3) All spotted frogs lived in the Deep Creek drainage (see Fig. 1) above Lake Bonneville in western Bonneville Basin where they occur today. After the lake stopped rising, these frogs moved along the shorelines of Lake Bonneville. The ideal time for this movement was during the relatively stable Provo level of Lake Bonneville, which lasted some 300 years after the high-water threshold broke in Idaho (Benson et al. 1990). The shoreline distance from the Deep Creek refugia to Tule Valley via the Provo level approximates 340 km, which includes movement around the northern end of the Fish Springs range. This distance is feasible under conditions of movement in the Wyoming (Turner 1960, Carpenter 1954). During wet years shorter routes over low passes might be feasible.

In view of the above discussion of the unique hydrology of Tule Valley in which spotted frogs survived for 14,000 years, one might ask, Is their survival assured in the future? Presently, Tule Valley springs are in a comparatively natural state. Water is pumped for livestock and formerly for oil-well exploration from Coyote Complex (#26) and North Tule (#11). Bulrushes have been burned annually by livestock operators. Limited livestock grazing occurs, resulting in holes punctured in the aquatic habitats, which greatly diminish the size of the habitats. This is the most severe impact on the aquatic habitats. Members of the Centrarchidae (sunfish) were [illegible] introduced in North Tule #11 and [illegible] once grew in South Central #15 [illegible] North Tule #11 (Fautin 1946), and [illegible] and trunks exist. A mining [illegible] North Tule Complex for industrial [illegible]. Military low-flying supersonic [illegible] in Tule Valley and adjacent [illegible]; however, the effect of sonic booms [illegible] unknown. On the positive side, the [illegible] Management enclosed the [illegible] #15, North Tule #12, and [illegible] in fences to protect the aquatic habitats from livestock. And the carbonate soils, the spring source of water, and the groundwater recharge of the water will protect frogs from anthropogenic air and land pollution.

Spotted frog habitats in Tule Valley thus stand in sharp contrast to spotted frog habitats along the Wasatch Front in eastern Bonneville Basin. Along the Wasatch Front the spotted frog is no longer found in many historic locations. Suggested impacts include (1) fragmentation of habitat by highway culverts, dams, reservoirs, and urbanization; (2) destruction of habitats by reservoirs, channeling of rivers, diversion of waters for irrigation, and preventing flood plains from being flooded; and (3) impacts of man on these habitats by utilization of livestock in riparian and wetland zones and introduction of raccoons, bullfrogs, crayfish, bass, and trout to these habitats. Again, the unique aspects of Tule Valley, namely, the locations of spotted frog habitats on the valley floor, the saline nature of the habitats, and the isolated nature of Tule Valley itself, have prevented much of the habitat destruction that has occurred along the Wasatch Front.

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GROWTH OF SMALLMOUTH BASS (*MICROPTERUS DOLOMIEU*) IN FLAMING GORGE RESERVOIR, WYOMING-UTAH

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ABSTRACT.—Growth of smallmouth bass (*Micropterus dolomieu*) was described for three widely spaced areas progressing [illegible] Flaming Gorge Reservoir, Wyoming-Utah. Significant differences among areas were detected only for age-1 fish. Growth in the reservoir was compared with that of populations in other lentic habitats of varying growing season lengths in North America; slow growth in the reservoir was related to the relatively short growing season (less than 90 days).

Key words: smallmouth bass, Micropterus dolomieu, *growth, population structure, reservoir.*

The native range of smallmouth bass (*Micropterus dolomieu*) extended from Ontario, Canada, south to northern Georgia and Alabama, west to Oklahoma and southeastern Kansas, and northeast to South Dakota. Since the mid-1800s this species has been introduced to the western United States and Canada, greatly expanding its range (Robbins and MacCrimmon 1974, Lee et al. 1980).

Although not native to Wyoming and Utah, the smallmouth bass has also established there (Baxter and Simon 1970). In 1967 it was introduced to Flaming Gorge Reservoir, Wyoming-Utah (Pettengill et al. 1983). Flaming Gorge Reservoir (1841 m MSL when filled) has an agricultural growing season of < 90 d (Koss et al. 1988). Natural recruitment of *Micropterus* spp. has not been observed > 1900 m MSL in Wyoming (Hubert 1988). Short growing seasons above this elevation probably lead to winter mortality of young-of-year (Shuter et al. 1980). Flaming Gorge Reservoir is at the highest elevation in Wyoming where successful smallmouth bass reproduction is known to occur.

The northern limit of the native range of smallmouth bass occurs where the growing season is about 120 d (Robbins and MacCrimmon 1974), and populations there have relatively slow growth (Doan 1940, Watson 1955, and Turner and MacCrimmon 1970). Growth rate of the species varies over its natural and introduced range and is at least partially related to growing season length (Bennett 1938, Tate 1949, Coble 1967, and Hubert 1975). Shorter growing seasons limit the time that fish have to actively feed and grow each year. Published assessments of smallmouth bass growth rates are from areas where the agricultural growing season is >90 d.

Lack of smallmouth bass population dynamics information in Flaming Gorge Reservoir and other waters in the western United States prompted this study. We assessed growth in three widely spaced areas in Flaming Gorge Reservoir to determine if differences occur. We hypothesized that growth in the reservoir might differ longitudinally due to the decline in biological productivity from headwaters to the dam (Varley 1967, Wiley and Varley 1978). We also assessed the influence of elevation and growing season on growth relative to other populations, and we hypothesized that growth in Flaming Gorge Reservoir would be relatively slow.

STUDY AREA

The Green River, a tributary to the Colorado River, was impounded in 1962 to create Flaming Gorge Reservoir in southwestern Wyoming, Sweetwater County, and northeastern Utah, Daggett County. At full pool the reservoir is 147 km long and has a surface area of 17,000 ha. Two distinct topographic regions border the reservoir. The upstream two-thirds of the impoundment lies on an open plateau of sagebrush-covered rolling hills; the lower one-third

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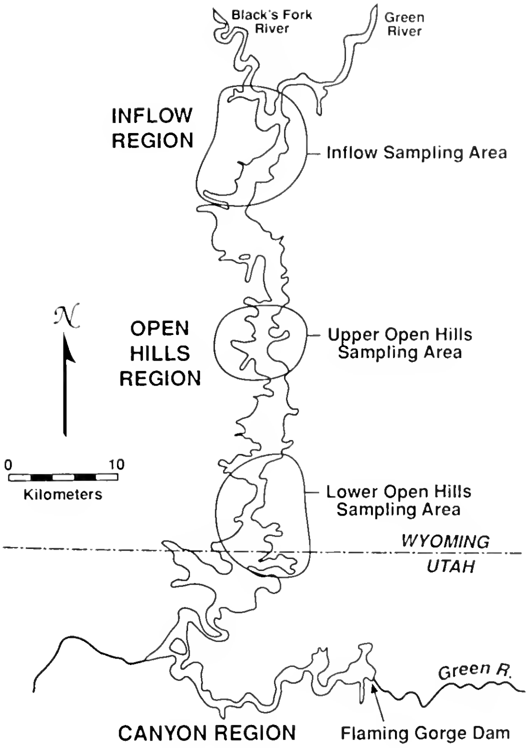

Fig. 1. Flaming Gorge Reservoir showing the locations of the three areas from which smallmouth bass were sampled.

is in a wooded area of high mountains and a deeply cut gorge (Varley 1979).

The reservoir is generally separated into three regions (Fig. 1) based on topography, geology, and hydrographic features (Varley 1967, Wiley and Varley 1978, and Varley and Livesay 1976). Water quality grades from eutrophic at the headwaters to almost oligotrophic near the dam (Varley 1967). The inflow region (northernmost 32 km) is influenced by the Green and Black's Fork rivers. Water temperature there is warmer than downstream, an oxygen-deficient zone sometimes occurs, and maximum depth is 24 m. The open hills region extends 48 km downstream from the inflow region. It is characterized by extensive bays and littoral shelves; maximum depth is 61 m. Thermal stratification is not prevalent because of wind action. The canyon region extends 39 km from the open hills region to the dam. This region is narrow with sheer walls, water is well oxygenated and thermally stratified, and maximum depth is 122 m.

METHODS

Smallmouth bass were collected 5–20 June 1991 from one sampling area in the inflow region and two sampling areas in the open hills region (Fig. 1) using boat-mounted electrofishing gear. Total length (TL) was measured, and scales were collected from each fish following the methods of Jearald (1983). Scales were read (19X) using a microfiche reader, and age of each fish was estimated from scale annuli. Fish length at each annulus was back-calculated using a 35-mm intercept value as suggested by Carlander (1982).

Mean TLs at each annulus were assessed for differences among sampling areas using one-way ANOVA (Sokal and Rohlf 1981). A chi-square test for heterogeneity was used to determine differences in age structure among sampling areas.

Linear-regression analysis was used to assess the relation between mean TLs of age-4 smallmouth bass and agricultural growing season length for 31 lakes and reservoirs across North America. A sample of 25 smallmouth bass from the downstream end of Flaming Gorge Reservoir was also included (Pettengill et al. 1983). Age-4 fish were compared because this age group occurred in all populations described in the literature we used, and back-calculated lengths are less affected by the method of calculation at age 4 than at younger ages. The growing season length for lakes and reservoirs was determined using Koss et al. (1988). Lakes were classified in 30-d intervals, and the upper limit of each interval was used as the independent variable in the regression analysis.

Statistical calculations were performed using STATISTIX 3.1 (Analytical Software 1990), and significance was determined at $P \leq .05$.

RESULTS

Mean back-calculated TLs at each age for the smallmouth bass collected from each of the three sampling areas in the reservoir were compared (Table 1). ANOVA indicated a significant difference ($P = .011$) among locations only for age-1 fish. Age structure of smallmouth bass from the three areas was computed (Table 1), and a chi-square test indicated no significant differences in age distributions among areas.

[illegible] annulus formation of smallmouth bass collected from three sampling [illegible] (UOH), and lower open hills (LOH) in Flaming Gorge Reservoir, Wyoming-Utah.

[illegible]	[illegible]	Sample [illegible]	Mean total length (mm) at each annulus											
			I	II	III	IV	V	VI	VII	VIII	IX	X	XI	XII
[illegible]	INF	1	95											
	UOH	[illegible]	97											
	LOH	5	86											
[illegible]	INF	17	99	136										
	UOH	[illegible]	102	149										
	LOH	9	85	122										
[illegible]	INF	25	97	128	157									
	UOH	2	99	134	182									
	LOH	16	89	128	159									
1987	INF	13	106	142	178	201								
	UOH	4	98	142	178	222								
	LOH	17	96	136	169	199								
1986	INF	12	104	141	176	206	209							
	UOH	6	102	142	186	221	263							
	LOH	18	106	142	180	215	247							
1985	INF	10	121	152	182	211	239	263						
	UOH	6	108	143	171	201	230	263						
	LOH	15	102	131	157	190	219	252						
1984	INF	12	100	130	160	190	219	241	270					
	UOH	8	106	141	178	213	245	274	258					
	LOH	9	111	147	174	208	243	279	296					
1983	INF	14	99	135	166	199	228	259	262	285				
	UOH	3	104	134	160	188	226	259	293	329				
	LOH	2	112	149	177	208	243	279	296	316				
1982	INF	7	103	139	166	193	219	239	265	293	317			
	UOH	2	102	143	177	210	250	288	323	347	368			
	LOH	4	100	133	160	188	221	246	203	226	242			
1981	INF	9	104	135	163	193	223	250	277	303	330	350		
	UOH	1	115	163	216	269	306	338	354	365	375	391		
	LOH	2	105	134	167	215	253	282	302	325	353	381		
1980	INF	1	100	129	149	164	194	214	234	259	288	318	348	
	UOH	1	100	133	176	214	236	258	285	328	356	372	394	
	LOH	3	104	140	186	211	244	273	304	329	350	372	394	
1979	INF	1	101	134	163	188	208	227	247	267	301	326	341	361
	UOH	0												
	LOH	0												
	INF	[illegible]	103	137	166	194	217	242	259	284	302	331	344	361
	UOH	[illegible]	105	142	180	217	251	280	302	342	366	382	394	
	[illegible]	[illegible]	100	136	170	204	239	268	284	299	315	377	394	

[illegible] smallmouth bass [illegible] was used to evaluate the [illegible] on growth of smallmouth [illegible] .30, P .0012 [illegible] obtained:

Mean length [illegible] 77 days), where days is the upper limit of the 30-d interval in which the various populations occurred (Fig. 2). As growing season length increased, mean TL of smallmouth bass at age 4 increased. The two Flaming Gorge Reservoir studies were the only ones where a 90-d growing season occurred, and they had the smallest fish at age 4.

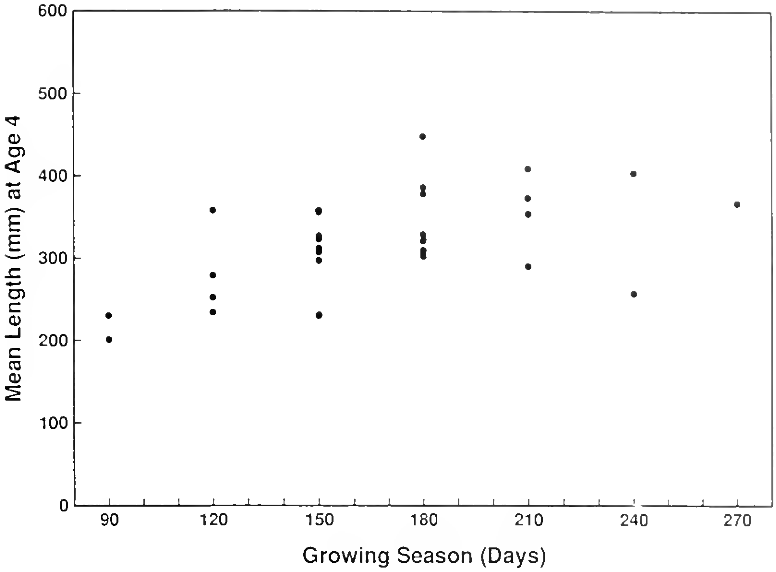

Fig. 2. Mean total lengths at age 4 for smallmouth bass from 31 lakes and reservoirs with varying growing seasons. All lakes and reservoirs with growing seasons within a 30-day interval were plotted at the upper limit of the interval. The lakes and reservoirs included the following: **90 d**—Flaming Gorge Reservoir, Wyoming (present study, Pettengill et al. 1983); **120 d**—Owen Lake, Wisconsin (Bennett 1938); Shadehill Reservoir, South Dakota (Willis et al. 1990); Big Lake, Maine (Watson 1955); and Weber Lake, Wisconsin (Bennett 1938). **150 d**—Tedenac Lake, Ontario (Turner and MacCrimmon 1970); Lake Opeongo, Ontario (Doan 1940); Winola Lake, Pennsylvania (Carlander 1977); Cayuga Lake, New York (Webster 1954); Oneida Lake, New York (Forney 1961); Lewis and Clark Reservoir, South Dakota (Willis et al. 1990); Lake McConaughy, Nebraska (McCarraher et al. 1971); Hiwassee Reservoir, North Carolina (Strond 1949); and Claytor Lake, Virginia (Roseberry 1951). **180 d**—Santeehlah Lake, North Carolina (Messer 1961); Clarke Lake, Pennsylvania (Carlander 1977); Malcomsen's Pond, Illinois (Bennett and Childers 1957); Connowingo Pond, Maryland (Heisey et al. 1980); Clearwater Lake, Missouri (Patriarche and Campbell 1958); Quabbin Lake, Maine (McCaig and Mullan 1960); Norris Reservoir, Tennessee (Strond 1948); Allerton Lake, Illinois (Bennett and Childers 1957); Lock Raven Reservoir, Maryland (Carlander 1977); and Centerhill Reservoir, Tennessee (Hargis 1965). **210 d**—Little Lake, Oklahoma (Finnell et al. 1956); Pickwick Reservoir, Alabama (Hubert 1975); Lake Eucha, Oklahoma (Jackson 1966); and Ouachachita Lake, Arkansas (Hulsey and Stevenson 1958). **240 d**—Fort Gibson Lake, Oklahoma (Carlander 1977); and Folson Lake, California (Tharratt 1966). **270 d**—Pine Flat Lake, California (Emig 1966).

DISCUSSION

Among the three sampling areas, the mean length at each age did not differ significantly except for age-1 smallmouth bass. The smallest age-1 fish were in the most downstream sampling area, which was least eutrophic. Young smallmouth bass in lentic habitats begin feeding on zooplankton; then insects become important in the diet, and finally crayfish and fish (Coble 1975). Possibly, food resources for small fish were less abundant in the most downstream sampling area. Lack of significant differences in TLs of age-2 and older fish may be due to similar abundance of crayfish and forage fishes among the sampling areas, or to the ability of larger fish to move among areas.

At the northern edge of their native range, smallmouth bass grow considerably faster than in Flaming Gorge Reservoir, probably due to differences in growing season length (Fig. 2). For example, growth rates were much faster in Tedenac Lake, northern Ontario, Canada (Turner and MacCrimmon 1970), and Big Lake, Maine (Watson 1955), than in Flaming Gorge Reservoir. Smallmouth bass in southern reservoirs, such as Pickwick, Tennessee (Hubert 1975), Centerhill, Tennessee (Hargis 1965), and Folsom, California (Tharratt 1966), increased in TL at twice the rate observed in Flaming Gorge Reservoir.

Smallmouth bass in southern waters grew faster (Bennett 1938, Coble 1967), but Strond (1948) concluded the faster growth in warmer waters also contributed to earlier death. Small-

smallmouth bass in Flaming Gorge Reservoir grew slowly, and fish up to age 12 were recorded. The maximum recorded age for smallmouth bass is 15 years (Stone et al. 1954, Scott and Crossman 1973). When the population structure of smallmouth bass in Flaming Gorge Reservoir is compared with that in other waters, it is evident that fish in Flaming Gorge Reservoir live longer than those in most other waters.

Despite the elevation of Flaming Gorge Reservoir, the smallmouth bass population is self-sustaining. However, growth rate is among the slowest recorded. Many factors could cause this (Brown 1960, Coble 1967, Keating 1970, and Forney 1972), and our analysis indicates that a short growing season is a significant limiting factor. The smallmouth bass population in Flaming Gorge Reservoir may have the shortest growing season of any self-sustaining population, and the slowest growth on record for a lake-dwelling population.

ACKNOWLEDGMENTS

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AUTUMN AND WINTER FOODS OF THE LESSER PRAIRIE-CHICKEN (*TYMPANUCHUS PALLIDICINCTUS*) (GALLIFORMES: TETRAONIDAE)

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[illegible] Descriptions of Lesser Prairie-Chicken (*Tympanuchus pallidicinctus*) foods in New Mexico have not [illegible] between autumn and winter seasons. We analyzed and compared prairie-chicken crop contents in [illegible] and 1977 ($n = 17$) and winter 1977 ($n = 4$) and 1978 ($n = 2$) in a shinnery oak (*Quercus havardii*) [illegible] southeastern New Mexico. Autumn foods were a mixture of seeds ($\bar{x} = 43\%$), vegetative material ($\bar{x} = 39\%$), and [illegible] especially shinnery oak acorns and insect galls ($\bar{x} = 49\%$). Short-horned grasshoppers (Acrididae, [illegible]) were an important food. Winter foods were shinnery oak acorns ($\bar{x} = 69\%$) and wild buckwheat (*Eriogonum* [illegible]). Use of vegetative material and insects decreased from autumn to winter, whereas use of acorns increased. High Plains Bluestem Subtype in the Southern Mixed Prairie is an important habitat that provides many of the [illegible] eaten by prairie-chickens. Therefore, broad-scale disturbances of this community should be avoided.

Key words: food, feeding, Lesser Prairie-Chicken, New Mexico, shinnery oak, Tympanuchus pallidicinctus.

Lesser Prairie-Chickens (*Tympanuchus pallidicinctus*) occupy semiarid grasslands that typically include a large component of shrubs, either shinnery oak (*Quercus havardii*) or sand sagebrush (*Artemisia filifolia*). A description of foods used by prairie-chickens in the shinnery oak grasslands is incomplete. Davis et al. (1981) compared spring and summer diets in shinnery oak grasslands of eastern New Mexico. They found that prairie-chickens feed on green, leafy vegetation in spring but change to insects in summer. Frary (1957) found that insects are important in early autumn (Sep–Oct) in eastern New Mexico. Crawford and Bolen (1976) evaluated autumn diets of 90 Lesser Prairie-Chickens collected in mid-October from shinnery oak habitats of west Texas. Despite the fact that their study area included cultivated grains, shinnery oak and insects were the principal natural foods.

A [illegible] description and comparison of [illegible] Lesser Prairie-Chickens in shin[illegible] through the entire annual cycle could [illegible] assist land managers in manipulating [illegible] food resources throughout the year. [illegible] published descriptions of Lesser [illegible] foods in shinnery oak grasslands [illegible] differentiate between autumn and winter. The purpose of this study was to provide a description of autumn and winter foods of Lesser Prairie-Chickens. The objectives were to collect crops of prairie-chickens during autumn and winter, to analyze crop contents to determine the type and amount of foods consumed, and to compare and contrast diets between seasons and years.

STUDY AREA

The study area is approximately 15,500 ha of Bureau of Land Management lands in Chaves County in southeastern New Mexico. Topography is gently undulating. Climate is semiarid with distinct seasons and wide ranges of diurnal and annual temperatures. Nearly 75% of the annual precipitation (30-year $\bar{x}$ = 345 mm/yr) falls during the growing season, May through October, mainly from brief but often intense thunderstorms (U.S. Department of Commerce 1976, 1977).

The study area is in the Southern Mixed Prairie Type, where the High Plains Bluestem Subtype grades westward into the Desert Prairie Subtype (Holechek et al. 1989:79). Most of the study area (89%) is on deep, sandy soils

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where vegetation is dominated by various combinations of bluestem grasses (*Andropogon hallii* and *A. scoparius*) and shinnery oak that characterize the High Plains Bluestem Subtype. The remaining 11% of the area comprises scattered inclusions of tighter soils where vegetation is dominated by short grasses, especially grama (*Bouteloua* spp.) and buffalograss (*Buchloe dactyloides*), characteristic of the Desert Prairie Subtype. Snakeweed (*Xanthocephalum sarothrae*) and mesquite (*Prosopis glandulosa*) are conspicuous invaders of this subtype in some parts of the study area.

METHODS

Crop contents were from birds collected during autumn (Oct–Dec 1976, $n = 9$, and 1977, $n = 17$) and winter (Jan–Feb 1977 and 1978, $n = 6$), mostly by shotgun or small-caliber rifle. Two were taken from birds that died as a result of trapping in autumn 1977, and two were donated by hunters in autumn 1978. Data from empty crops were not used in the analysis. We stored the frozen crops in 100-ml plastic storage bottles until analysis. Contents from each crop were analyzed separately. Foods were measured by volumetric displacement to the nearest 0.1 ml, and items measuring <0.1 ml were classified as "trace." Composition of diet was determined by the aggregate percent method (Martin et al. 1946). We used Borror and White (1970) and Correll and Johnston (1970) to identify food items.

Means and standard errors were calculated when an individual food item was detected in two or more crops. Small sample sizes reduced the power of statistical tests, but we used Student's t test to test the hypothesis that there were no differences in the composition of food items between seasons and years (Snedecor and Cochran 1989). Differences were considered significant at $P < .05$.

RESULTS

Autumn diets primarily consisted of shinnery oak acorns, short-horned grasshoppers (Acrididae), broom groundsel (*Senecio spartioides*) leaves, and insect galls from shinnery oak (Table 1). Thirty different food items were identified, nearly half of which were green vegetation. Crop contents from birds collected by hunters and from birds that died as a result of trapping were similar to those collected by other methods within the same season.

Between-year differences were noted for autumn diets (Table 1). Use of mast and seeds (primarily shinnery oak acorns) in 1976 diets ($x = 65\%$) was significantly greater ($P < .05$) than in 1977 ($x = 21\%$). Insects ($x = 30\%$, primarily short-horned grasshoppers) and a variety of vegetative material ($x = 49\%$) comprised a greater ($P < .05$) proportion of diets in 1977 than in 1976 (animal material $x = 7\%$, vegetative material $x = 28\%$).

Winter samples were combined between years because of the small sample size (1977 $n = 4$, 1978 $n = 2$). Foods consumed by Lesser Prairie-Chickens in winter primarily consisted of shinnery oak acorns ($x = 69\%$), with lesser amounts of green vegetation ($x = 26\%$) and insects ($x = 5\%$, Table 1). No differences ($P > .05$) were detected in crop contents between autumn 1976 and winter 1977–78. Shinnery oak acorn composition of winter crops ($x = 69\%$) was greater ($P < .05$) than in autumn 1977 crops. Use of vegetative material and insects (resulting primarily from lack of short-horned grasshoppers in winter) was lower ($P < .05$) in winter crops than in crops collected in autumn 1977.

DISCUSSION

Differences in autumn diets of prairie-chickens between years might be explained by the fact that annual precipitation was nearly 100 mm (27%) below normal in 1977 ($x = 250$ mm; U.S. Department of Commerce 1976, 1977). Lower-than-normal precipitation in 1977 might have affected the availability of food resources.

Shinnery oak provided acorns, insect galls, and leaves, which together constituted 50% of the autumn diet in our study and 36% of natural foods in Crawford and Bolen's (1976) study. Despite the fact that Crawford and Bolen's (1976) study area included grain fields, shinnery oak was the principal natural food in autumn. In both studies short-horned grasshoppers were the principal animal food in autumn. Frary (1957) reported crop contents from 17 Lesser Prairie-Chickens collected in eastern New Mexico about 45 km northeast of our study area. His sample was pooled across 6 months, and so seasonal comparisons with our data are not possible. He did find, however, that insects were important in early autumn (Sep–Oct).

[illegible] (Oct–Dec) and winter (Jan–Feb) crop contents of Lesser Prairie-Chickens, [illegible]

[illegible]	Autumn 1976 (n = 9)	Autumn 1977 (n = 17)	Winter (n = 6)
Mast material			
[illegible]			
[illegible]	61 (12.7)[a]	17 (6.9)	69 (6.4)
[illegible] spp	4 (2.2)		
[illegible]		4	
[illegible]	t[b]		
Total	65 (13.0)	21 (6.8)	69 (6.4)
Vegetative material			
Quercus havardii			
Insect galls	14 (8.2)	5 (1.7)	
Leaves	1	2	
Senecio spartioides		12 (6.1)	5 (3.4)
De[illegible]	6 (5.0)	7 (2.4)	
Eriogonum annuum		7 (2.7)	14 (4.2)
Phlox spp	4 (1.9)		4 (2.0)
Lithospermum incisum		4	t[b]
Composite		4	
Oenothera spp		4	t[b]
Euphorbia spp	3	1	t[b]
Hymenopappus spp		2	t[b]
Xanthocephalum sarothrae		1	t[b]
Penstemon buckelyi		t[b]	2
Others	t[b]		t[b]
Total	28 (13.8)	49 (9.3)	26 (6.3)
Animal material			
Acrididae	2 (1.4)	28 (8.2)	
Gryllidae	3 (0.3)		
Lepidoptera	2		
Carabidae		t[b]	5 (3.6)
Others	t[b]	2	t[b]
Total	7 (3.6)	30 (8.2)	5 (3.7)

[a] [illegible]

[b] [illegible]

Similarities between autumn 1976 and winter 1977–78 diets probably were a result of the fact that most (4/6) crops collected in winter were from 1977 and the availability of acorns [illegible] between seasons. Differences between autumn 1977 and winter 1977–78 diets [illegible] from the fact that winter diets [illegible] of winter 1977 than [illegible] precipitation in 1977 [illegible] production in the [illegible] and on other food [illegible] (1957) found that [illegible] winter diets and that [illegible] winter. Jones (1963) [illegible] in Oklahoma showed [illegible] seeds in the winter diet

MANAGEMENT IMPLICATIONS

Lesser Prairie-Chickens are closely associated with the shinnery oak–grassland community in much of their occupied range. Within this community, in New Mexico, Lesser Prairie-Chickens obtain most of their autumn and winter diets from a rather small number of plants and associated insects that are common in the less grassy habitat. Shinnery oak is the most heavily utilized food of prairie-chickens on an annual basis. Shinnery oak acorns, catkins, leaves, and galls in various combinations provide adult birds with >50% of their diet in autumn and winter. Because of the importance of shinnery oak grassland to prairie-chickens for both food and cover, broad-scale eradication of this community should be avoided.

Acknowledgments

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ESTABLISHMENT OF SHOSHONE SCULPIN (*COTTUS GREENEI*) IN A SPRING INHABITED BY MOTTLED SCULPIN (*C. BAIRDI*)

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Abstract.—The Shoshone sculpin (*Cottus greenei*) is found only in springs of the Thousand Springs formation along the Snake River in Idaho. In 1983 a small population of Shoshone sculpin was introduced into an unnamed spring in the Thousand Springs formation in an attempt to increase the range of the species. Previously, the only sculpin in that spring was the mottled sculpin (*Cottus bairdi*). The Shoshone sculpin was able to establish itself and become the predominant fish within 8 years.

Key words: Shoshone sculpin, Cottus greenei, *mottled sculpin,* Cottus bairdi, *sympatric species, species of special concern, Snake River, Idaho.*

As of 1982, the Shoshone sculpin (*Cottus greenei*) was found in only 25 of 40 spring systems in the Thousand Springs formation near Hagerman in south central Idaho (Wallace et al. 1984). The species principally inhabits springs entering the north side of the Snake River from river kilometer 910.4 (relative to the mouth of the Snake River) upriver to kilometer 950.4. Because of its limited range and the extent of habitat modification, the Shoshone sculpin was proposed as a threatened or endangered species (Williams 1980). It is currently a candidate threatened or endangered species (W. E. Martin, U.S. Fish and Wildlife Service, Portland, Oregon, personal communication). The American Fisheries Society considers it "threatened" (Williams et al. 1989), and Idaho Department of Fish and Game considers the Shoshone sculpin a "priority species of special concern" (Moseley and Groves 1992).

Shoshone sculpins occur sympatrically with mottled sculpins (*Cottus bairdi*) in 16 spring systems in the Thousand Springs formation (Wallace et al. 1984). Larger mottled sculpin are [illegible] on smaller sculpin (Bailey 1952, Wydoski and Whitney 1979) and are considered [illegible] of Shoshone sculpin. The purpose of this study was to assess the extent to which Shoshone sculpin could be successfully introduced into an environment that seemed physically adequate but was already occupied by mottled sculpin.

METHODS

Shoshone sculpins were introduced into a small unnamed spring pond as part of an Idaho Department of Fish and Game nongame program to reestablish them in portions of their original range (Griffith and Daley 1984). The spring pond, referred to here as Transplant Spring, is 15.3 km upriver from Briggs Springs, the nearest spring inhabited by Shoshone sculpin at the time (Wallace et al. 1984).

Transplant Spring is approximately 1000 m^2 in surface area and enters the Snake River at river kilometer 965.7 in Gooding County, Idaho. Water flows from the spring head near the base of a basalt cliff over a 20-m-long cascade into a pond that is impounded by a set of culverts. The stream drops vertically 2 m into the Snake River after passing through the culverts. The discharge of Transplant Spring is influenced by a fish hatchery water diversion near the spring head.

Boulder and cobble substrate near the cascade shift to gravel, sand, and silt at the tail of the pool. There are dense patches of water speedwell (*Veronica* sp.) and cattail (*Typha* sp.). Amphipods, a group shown to be heavily consumed by Shoshone sculpin (Connolly 1983), were abundant (1000–5000 per m^2) during the study. Taxa such as dipterans, trichopterans, and oligochaetes that also are utilized by Shoshone sculpin were present in densities similar to those

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TABLE 1. Number of sculpins collected per 1-m^2 frame net and relative abundance (RA; electrofishing samples) and percent *Cottus greenei* of total *Cottus* sp. at Transplant Spring, Idaho, 1983–91. Only fish ≥ 20 mm TL were included. On 15 August 1983, 419 *C. greenei* were introduced into Transplant Spring.

		Cottus greenei			*Cottus bairdi*	
Date	Method	Number collected	Number per frame	% total	Number collected	Number per frame
13 Aug 1983	11 frame nets	0	0	0	30	1–6
20 Nov 1983	10 frame nets	4	0–2	15	23	0–6
18 Feb 1984	RA	1	—	5	21	
21 Apr 1984	RA	0	—	0	15	
24 Sep 1984	RA	12	—	27	33	
3 Oct 1990	RA	20	—	100	0	
28 Sep 1991	4 frame nets and RA	96	3–29	98	2	0

in other springs supporting dense sculpin populations. Other fish species captured in Transplant Spring were mottled sculpin, rainbow trout (*Oncorhynchus mykiss*), and peamouth (*Mylocheilus caurinus*).

Shoshone sculpins (n = 419; mean length 36 mm TL, range 18–70 mm) were dip-netted and seined from Bickel Spring at the Hagerman National Fish Hatchery 25 km downriver from Transplant Spring on 15 August 1983 and stocked at Transplant Spring within a few hours. The sculpin population in the spring was monitored in August 1983 prior to the introduction, and after the introduction in November 1983, February, April, and September 1984, October 1990, and September 1991. The 1983 and 1991 samples were quantitative estimates using a frame net at 4–11 random sites. The 0.75-m-high boxlike PVC frame has 1-m^2 openings at the top and bottom, with 3-mm-diameter mesh netting attached to the sides. In the 1983 frame net samples, electrofishing (a Coffelt model BP-1C unit producing pulsed direct current) and dip nets were used simultaneously to capture fish within the frame net. In the 1991 frame net samples, the electrofisher was not employed within the frame net; instead, two dip nets were used until both netters made three consecutive passes without capturing a fish. On other sampling dates and in areas not sampled by the frame net, the electrofisher and dip nets were used to assess relative abundance of fishes.

Sculpins were identified and measured (TL) by viewing them through a water-filled plexiglas measuring board. This aquarium-like device enabled us to discriminate these small, morphologically similar fish while minimizing handling stress prior to release. Sculpins less than 20 mm TL, which are age-0 fish (Connolly 1983), were not included in the analysis because they were not monitored in the 1983 and 1984 samples.

RESULTS

On 13 August 1983, prior to the stocking of Shoshone sculpins, mottled sculpins were in all frame net samples and distributed throughout the spring pond. Most individuals were small or intermediate in size (33–97 mm TL). An average of 2.7 mottled sculpins was captured per frame net sample (Griffith and Daley 1984).

After the introduction of the Shoshone sculpin, 27 individuals were collected in 1983 and 82 in 1984 (Table 1). Mottled sculpins were present at both the vegetated habitats and the rocky habitats in 1983 (Griffith and Daley 1984). The abundance of Shoshone sculpins relative to the total number of sculpins, both Shoshone and mottled, was 15% in 1983 and 16% in 1984. Five age-0 Shoshone sculpins were found in September 1984 (Griffith and Daley 1984), indicating that some Shoshone sculpins reproduced successfully. On 3 October 1990, 20 sculpins were collected, all of which were Shoshone sculpin, ranging from 28 to 70 mm TL.

On 28 September 1991, 100 Shoshone sculpins were collected from frame net samples and electrofishing (Table 1). In four frame samples there were 53 mature (up to 80 mm TL) and 4 age-0 (≤ 20 mm TL) Shoshone sculpin, averaging 14.3 ± 11 (mean ± standard deviation) individuals/m^2. Forty-three other Shoshone sculpin were electrofished along the perimeter of the pond. Highest Shoshone [illegible] *Veronica*, where [illegible] approximately 20 fish. Two mottled sculpins were found in cobbles and boulders where the spring [illegible] into the pond.

Discussion

Shoshone sculpin has become the predominant fish in Transplant Spring in less than an 8-year period. That period represents two or three generations, based on typical longevity of 3-4 years (Connolly 1983). Reproduction was successful in 1984, but a substantial increase in population size was not recognized until 1990. Unfortunately, we have no data from 1985 to 1989 to assess the rate of change. Frame net sampling was probably more thorough in 1991 than methods used in 1983, which may have underestimated densities, although we believe the bias was minor.

A smaller, unnamed spring entering the Snake River 0.1 km downstream from Transplant Spring also was colonized recently by Shoshone sculpins. Nine fish were captured there with an electrofisher in September 1991. When the spring was sampled in 1981–83, only mottled sculpin and rainbow trout were found there (Griffith unpublished data). We suspect that Shoshone sculpins may have migrated the short distance downstream from Transplant Spring.

Shoshone sculpins introduced to Transplant Spring were able to reproduce, compete, and survive in the spring environment in the presence of the larger mottled sculpins. Other sympatric sculpins show habitat segregation by selecting different substrates, water velocities, depths, or temperatures. In Oregon streams the reticulate sculpin (*Cottus perplexus*) occupied riffles and pools in the absence of other sculpin species (Finger 1982). In the presence of the Paiute sculpin (*Cottus beldingi*), the larger reticulate sculpin used pools more frequently. Matheson and Brooks (1983) found that mottled sculpin in Virginia streams preferred colder water than did the Potomac sculpin (*Cottus girardi*), which occupied slow water velocity and silty substrates. In California the rough sculpin (*Cottus asperrimus*) selected deeper water (20 cm) than did the Pit sculpin (*Cottus pitensis*) and marbled sculpin (*Cottus klamathensis macrops*) (Brown 1991). Rough sculpins typically occupy spring-fed streams, and they are [illegible] to a narrow range of temperatures (Brown 1989). Rough and Shoshone sculpins both utilize the unique habitat provided by springs, and both have a limited geographic distribution.

Density data from Transplant Spring suggest that Shoshone sculpins may have been able to occupy or utilize habitat with lower water velocities and dense vegetation more effectively than mottled sculpins. Daley et al. (1982) observed that Shoshone sculpins rarely occupied areas with surface velocities greater than 60-80 cm/s. The highest densities of Shoshone sculpin typically occur in aquatic vegetation (Daley et al. 1982, and this report). When Shoshone sculpins were absent or less abundant in Transplant Spring, mottled sculpins utilized aquatic vegetation and low water velocity areas (Griffith and Daley 1984); apparently, however, they were displaced from this habitat, but not from the cascade at the pond head, by Shoshone sculpins.

Mottled sculpins primarily utilize rocky substrates and moderate water velocities (Bailey 1952, Wydoski and Whitney 1979, Page and Burr 1991). Mottled sculpins in North Carolina streams selected habitats with mean focal point velocities of 48-88 cm/s, and 71% of the sculpins occupied sites with overhead rocky shelters (Facey and Grossman 1992). It appears that Shoshone and mottled sculpins may segregate based partially upon water velocity.

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USE OF BOULDER POCKET HABITAT BY RAINBOW TROUT (*ONCORHYNCHUS MYKISS*) IN FALL RIVER, IDAHO

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Abstract.— Abundance of rainbow trout (*Oncorhynchus mykiss*) in relation to characteristics of pockets created by boulders was studied in Fall River, southeastern Idaho. To determine depth and surface area of pockets most selected by rainbow trout, fish were counted by snorkeling, and pocket physical dimensions were measured. An electivity index defined habitat selection in the following terms: the most suitable habitat was ≥0.7 m maximum depth, ≥0.5 m minimum depth, and ≥3 m² surface area. Some study reaches of Fall River had more suitable pockets available for trout than were being utilized.

Key words: rainbow trout, Oncorhynchus mykiss, *habitat use, Idaho, stream rehabilitation.*

Boulders create a major source of trout habitat in many higher-gradient western rivers. They create pools or pockets with increased depth and provide surface turbulence that may be the only cover available to trout. Water depth and boulder cover were important in determining density of trout in a Colorado stream (Stewart 1970). Boulder placement is a commonly used technique in stream rehabilitation (Rosgen and Fittante 1986) and may provide effective, durable trout habitat (Lere 1982).

This study evaluated age-1 and older wild rainbow trout (*Oncorhynchus mykiss*) use of boulder pocket habitat in Fall River, Idaho. Objectives were to determine the proportion of trout using boulder pocket habitat, and to assess the extent to which fish selected pockets of specific surface area and depth.

METHODS

The Fall River originates in the southwest portion of Yellowstone National Park. It flows east into Targhee National Forest, Idaho, and then through agricultural lands to join Henrys Fork of the Snake River approximately 10 km south of Ashton in Fremont County. The study area, at an elevation of about 1740 m, extends 7 km, half of this distance within the Targhee National Forest and half immediately below. The stream channel has been shaped by coarse-grained glacial outwash through which it flows. Basalt and ash flow tuff bedrock define the channel form. Sinuosity is low, approaching 1.0, and there are no meander pools. Overall gradient in the study reach is 0.64%.

Within-channel habitat was homogeneous and consisted predominantly of run habitat, as defined by Helm (1985). Little woody debris had been retained in the channel. At the 14–16 m³/sec low flows of late summer 1991, the stream margin had pulled away from any vertical banks formed by high flows, leaving no bank habitat to provide cover for larger trout. The study reach contained Paiute sculpin (*Cottus beldingi*), longnose dace (*Rhinichthys cataractae*), and a few Utah suckers (*Catostomus ardens*) and mountain whitefish (*Prosopium williamsoni*) in addition to the wild rainbow and occasional cutthroat (*Oncorhynchus clarki*) trout.

In August of 1990 and 1991 snorkel surveys were conducted to estimate trout density throughout the study area. These indicated that density of trout larger than age-0 averaged 0.35 fish/100 m², or approximately 136 fish/km (Griffith unpublished data). Three sites, representing a range of boulder pocket densities, were selected for the present study. Sites were 160–170 m long and averaged 26–46 m wide. A boulder was defined as ≥0.4 m diameter, situated so that its top was at or above the water

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[1] [illegible]
[2] [illegible] Idaho 83209

TABLE 1. Characteristics of boulder pockets used by 83 rainbow trout in three study sections of Fall River, Idaho, summer 1991.

Characteristic	Number of occupied pockets	Number of trout	Trout per pocket	
			Average	Range
Maximum depth (m)				
<0.46	0	0		
0.46–0.55	2	3	1.5	1–2
0.56–0.65	7	16	1.7	1–3
0.66–0.75	15	30	2.0	1–3
0.76–0.85	8	19	2.4	1–3
0.86–0.95	2	3	1.5	1–2
0.96–1.05	2	8	4.0	
1.06–1.15	1	4	4.0	
Minimum depth (m)				
<0.26	0	0	0	
0.26–0.35	1	1	1.0	
0.36–0.45	6	12	2.0	1–4
0.46–0.55	11	24	2.2	1–4
0.56–0.65	10	26	2.6	1–5
0.66–0.75	9	20	2.2	1–5
Surface area (m^2)				
<0.46	0	0		
0.46– 0.75	2	2	1.0	
0.76– 1.25	1	2	2.0	
1.26– 1.75	3	4	1.3	1–3
1.76– 2.25	2	3	1.5	1–2
2.26– 2.75	3	7	2.3	2–3
2.76– 3.25	6	13	2.6	1–4
3.26– 3.75	5	11	2.2	1–5
3.76– 4.50	4	8	2.0	1–3
4.51– 5.50	2	5	2.5	1–4
5.51– 6.50	1	2	2.0	
6.51– 8.50	2	4	2.0	
8.51–11.00	1	3	3.0	
11.01–13.50	1	2	2.0	
13.51–16.00	1	4	4.0	
16.01–20.50	1	3	3.0	
20.51–26.00	1	4	4.0	
26.01–30.00	1	5	5.0	

surface to create a pocket of lower velocity water immediately downstream. The low boulder density site (LBD) had 38 boulders that fit these criteria and averaged 0.5 boulders/100 m^2 of stream surface. The intermediate boulder density site (IBD) had 60 boulders (average 1.0 boulders/100 m^2), and the high boulder density (HBD) site contained 84 boulders (2.1 boulders/100 m^2).

During the last two weeks of August 1991, boulder locations in each site were mapped and trout focal point positions recorded by a snorkeler moving slowly upstream. Fish larger than about 15 cm were included, with most 15–25 cm and a few as large as 30 cm. No effort was made to differentiate fish by size categories. Underwater visibility was approximately 4 m, and water temperature ranged from 14° to 19° C from 1000 to 1500 MDT when observations were made.

After snorkeling, we recorded dimensions of all pockets in the section. We demarcated the lateral margins of a pocket by the abrupt change in water velocity that occurred there. Initially we used a velocity meter (Marsh-McBirney model 201) on a range of pockets in each site and then completed demarcation by eye. Water velocity, which ranged from 0.8 to 1.2 m/sec along the thalweg outside boulder pockets in all sites, was generally 0.3–0.5 m/sec within the pockets.

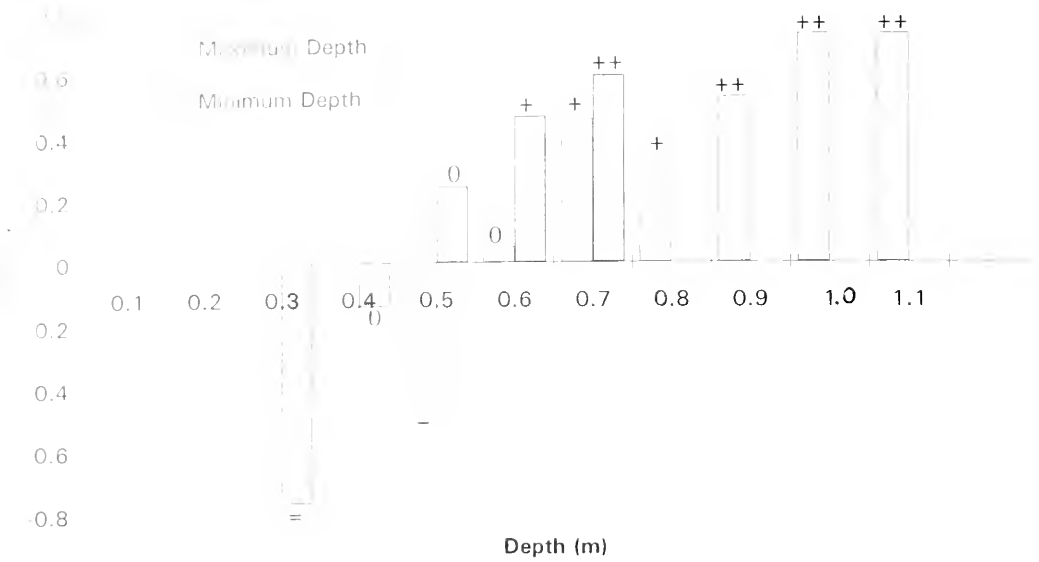

Fig. 1. Minimum depth (m) and maximum depth (m) of boulder pockets used by rainbow trout in Falls River, Idaho. Electivities are indicated: ++ (≥0.5, strong selection), + (>0.25 but <0.5, moderate selection), 0 (±0.25, no selection), – (>−0.5 but <−0.025, moderate avoidance), and = (≤ −0.5, strong avoidance).

To evaluate the selection by trout of the pocket parameters, an electivity index (D) was calculated:

$$D = \frac{r - p}{(r + p) - 2pr}$$

where r is the proportion of the resource used by rainbow trout and p is the proportion available in the environment (Baltz and Moyle 1985). Following Baltz and Moyle (1985), we interpreted strong selection to be indicated by D ≥ 0.5, moderate selection >0.25 but <0.5, no selection 0 ± 0.25, moderate avoidance >−0.5 but <−0.25, and strong avoidance ≤ −0.5. Electivity values were calculated for maximum and minimum depth and surface area of the boulder pocket.

RESULTS

There was a wide range of maximum and minimum depths and surface area of boulder pockets available on Falls River. Maximum depth among the three study sites ranged from 0.3 to 1.1 m and averaged 0.7 m. Minimum depth ranged from 0.2 to 0.7 m, averaging 0.45 m. Pocket surface area ranged from 0.25 to 28 m² [illegible] 4 m²). The larger and intermedi-[illegible] were primarily found in the HBD reach, and smaller pockets were primarily found in the LBD and IBD reaches.

Pocket surface area was partially a function of boulder diameter, with pocket area = 1.881 + 4.5572 × boulder diameter (R^2 = .57, N = 182) for all sites combined. The correlation was higher at lower boulder density sites; but at the HBD site, area of an individual pocket was also affected by the presence of adjacent boulders.

All trout observed in the study sites were in boulder pockets. Eighty-three fish were found, with 0, 17, and 66 at sites LBD, IBD, and HBD, respectively. The total number of boulder pockets holding trout was 10 (17% of pockets present) at IBD and 27 (32% of pockets present) at HBD. A comparison of utilized pocket measurements showed no significant difference between the two sites ($P < .05$) and the data were pooled for analysis.

As water depth and surface area of a pocket increased, the number of fish present generally increased (Table 1). No trout used pockets in which minimum depth was less than 0.26 m and maximum depth was less than 0.36 m.

As surface area increased, the number of fish per pocket generally increased to a maximum of 5 (Table 1). Average number of fish per pocket was 1.4 in pockets with surface areas <2.25 m², 2.2 in surface areas of 2.26–4.50 m², 2.2 in

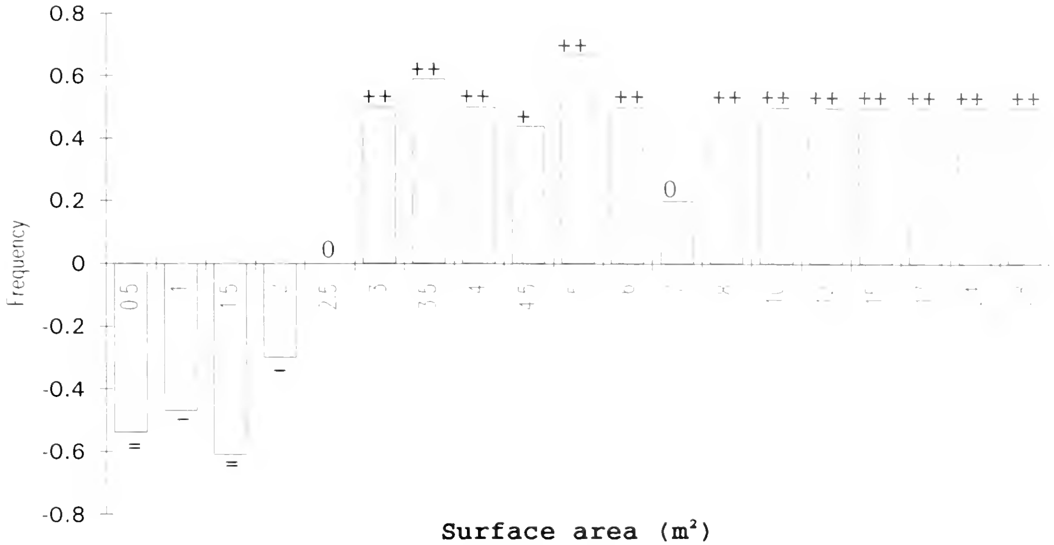

Fig. 2. Surface area (m^2) of boulder pockets used by rainbow trout in Falls River, Idaho. Electivities are indicated: ++ (≥0.5, strong selection), + (>0.25 but <0.5, moderate selection), 0 (±0.25, no selection), – (>–0.5 but <–0.025 moderate avoidance), and = (≤–0.5, strong avoidance).

surface areas between 4.51 and 8.50 m^2, and 3.5 in surface areas >8.5 m^2

The electivity index demonstrated that trout were selective in the microhabitat they occupied. Electivity values for maximum depth indicated moderate selection at depths equal to or greater than 0.7 m and strong selection at depths greater than 0.9 m (Fig. 1). Minimum pocket depth was not a sensitive index of trout density. At minimum depths of 0.6 m and deeper there was moderate selection and over 0.7 m, strong selection (Fig. 1). Pockets with surface areas equal to or exceeding 3 m^2 were moderately or strongly selected (Fig. 2).

Habitat for which rainbow trout showed a "strong" or "moderate" selection was viewed by us as the most suitable habitat for the study sites. Fifty of the 178 pockets in the three sites fell within those limits. Thirteen optimal pockets were located within the IBD reach and none within the LBD reach. Thirty-seven were located within the HBD reach, and more fish were found in that reach. A total of 23 of the 50 optimal pockets were not occupied by trout.

DISCUSSION

Maximum water depth in boulder pockets strongly influenced selection of habitat by rainbow trout in the Fall River. Baltz and Moyle (1985) evaluated rainbow trout habitat in a tributary of the Sacramento River, California, and found strong selection for depths greater than 0.6 m, similar to the threshold value for our study. The Habitat Suitability Index (HSI) for rainbow trout (Raleigh et al. 1984) indicates that depths greater than 0.46 m have a suitability index value of 1, the highest value possible. Not until Fall River pocket depths of ≥0.7 m were reached was there moderate to strong selection, and trout moderately avoided pockets at depths of 0.5 m; thus, the HSI did not accurately predict depth selection on Fall River. Minimum pocket depth appeared to be a less useful indicator of habitat selection for Fall River rainbow trout.

Pocket surface area was also a factor affecting trout density. Only four fish were found in pockets <1.5 m^2, and those >3 m^2 were selected. Lewis (1969) found that surface area and depth along with volume, current velocity, and cover accounted for 70–77% of the variation in numbers of trout in pools of Little Prickly Creek, Montana.

If surface area "requirements" reflect the size of territories defended by individual trout, in optimal habitat agonistic behavior by individual trout might serve to establish maximum [illegible] Allen (1969) and Grant and Kramer (1990) reviewed the literature for fluvial salmonids. Although data for rainbow trout were limited, strong similarities were found among the seven salmonid species they reviewed. For fish 15–20 cm long, average territory size in pools was approximately 1.5 m². In Fall River the estimated area occupied by individual trout, based on our observations of fish abundance per pocket, ranged from 0.5 to 6.0 m² and averaged 2.5 m². However, two-thirds of the fish were inhabiting areas < 2.5 m², suggesting that smaller territories might be required in boulder pockets than in the pools from which the data of Grant and Kramer (1990) were generated.

Lack of summer holding habitat in the LBD reach appeared to limit trout abundance, as the reach contained no quality pockets and no trout were present. Summer holding habitat did not appear to limit trout numbers in the HBD and IBD reaches because there were 23 pockets with optimal dimensions that were not utilized. Trout density in these reaches might have been depressed by low recruitment or factors such as winter mortality and food availability.

Although trout distribution is closely tied to physical habitat in Fall River, it is clear that simply adding boulders to rivers will not automatically increase trout populations. Pockets created by boulders must meet depth and surface area requirements before fish will inhabit them, as shown on Fall River. Other studies have found that water depth alone is not the major limiting factor for trout populations (Kennedy and Strange 1982); water velocity and available cover also influence trout density (Lewis 1969). These environmental requirements as well as other limiting factors must be understood before boulders are effectively used for habitat improvement.

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HUMORAL CREATININE IN WALLEYE (*STIZOSTEDION VITREUM*)

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ABSTRACT.—Published fish blood parameters are limited to commercially cultured species (e.g., rainbow trout [*Oncorhynchus mykiss*] and channel catfish [*Ictalurus punctatus*]). However, as walleye (*Stizostedion vitreum*) and other fish increase in value to the angler, hatchery and fish managers will require data on these species. Blood sera were collected from live walleye in the field, creatinine values were determined colorimetrically, and health range values were established from these data. Creatinine levels of walleye serum (0.06–0.72 mg/dl) were higher in three species but lower than recognized in a recent catfish study. Creatinine levels may be important in predicting diseases in which the kidney is adversely affected.

Key words: creatinine, walleye, Stizostedion vitreum, *health range, serum, colorimetric determination.*

The need for a rapid means of assessing the condition of fish exposed to environmental degradation and disease has long been recognized. Logically, blood is a medium with which to do this since no other single body tissue is more reflective of total body metabolism. Since our interests are in disorders of skeletal muscle, we elected to establish the range of serum creatinine levels, a nonprotein constituent in fish including feral walleye. Creatinine, an end product of creatine metabolism, is a normal and alkaline component of urine and blood. Warner and Williams (1977) recognized the need for an indicator in assessing the health of channel catfish and utilized blood serum components (i.e., metabolic products, electrolytes, enzymes). Field et al. (1943), Phillips (1958), Barnhart (1969), and Bentinck-Smith et al. (1987) determined ranges of variation in blood serum constituents in several fish species under different protocols (i.e., collecting, holding, rearing, etc.). According to Warner and Williams (1977), natural variation must be established before using these constituents to assess fish health. Hoffman (1963) and Wedemeyer and Chatterton (1971) defined natural variation as being ± two standard deviations of the mean value (normally distributed data) for healthy fish populations. In mammals, phosphocreatine spontaneously cycles at a slow rate to form creatinine, which is excreted in urine. The cycling rate depends upon the total phosphocreatine content (i.e., muscle mass) at a given temperature and pH (McGilvery and Goldstein 1979). Phosphocreatine acts in muscles of vertebrates as a reservoir of chemical energy for the phosphorylation of ADP to reconstitute ATP during muscle contraction. Since creatinine excretion depends upon phosphocreatine content, creatinine can be used to assess muscle mass. Creatinine is constant, with about 0.02 gm/kg of body weight excreted per day. Thus, when muscle degenerates from paralysis or muscular dystrophy, the creatinine content of urine falls (McGilvery and Goldstein 1979) because there is less muscle mass and phosphocreatine to spontaneously cycle to creatinine. Oser (1965) reported that creatinine in mammals is more readily excreted than uric acid or urea, and that even a slight increase in blood creatinine is evidence of impaired kidney function. In contrast with ammonia, which is excreted by the gills, creatinine is excreted by the kidney in fish (Smith 1929). Shell (1961) interpreted periods of increased creatinine concentration as indicating kidney impairment in smallmouth bass (*Micropterus dolomieu*). However, he concluded that cause-and-effect evidence linking the two phenomena is not available for fish as it is for mammals.

MATERIALS AND METHODS

Mature walleye (≥5 yrs of age) were collected by trap nets (1.8 × 2.4 m) and experimental gill nets (1.8 × 75 m; 19-, 25-, 38-, 51-, and 64-mm bar measure meshes) in April and May 1991

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[illegible] freshwater fish species. Values converted from mg % and mg/100 ml to

[illegible]	Health range 2 SD of mean	Mean mg/dl	SD	Range (mg/dl)
[illegible]				
[illegible]		0.056	—	0.042–0.087
[illegible]		0.072	—	0.051–0.085
[illegible] Madison, Wisconsin				
[illegible]				
[illegible]		0.041	—	—
[illegible]	—	0.049	—	—
[illegible] Cortland, New York				
[illegible] 1969				
[illegible] trout (n = 16)		0.105	—	0.053–0.20
[illegible] Lake, Bellvue, Colorado				
[illegible] and Williams 1977				
Channel catfish (n = 107)	0.00–0.37	0.178	0.96	—
Ponds at Gallatin, Tennessee				
Hille 1982				
Rainbow trout (n = ?)	—	—	—	0.02–0.217
Review paper including fish data collected in USA (Colorado) and Italy				
Bentinck-Smith et al. 1987				
Channel catfish (n = 376)	—	0.543	0.399	0.2–2.50
Rearing ponds, Stoneville, Mississippi				
Holloway and Shoemaker (unpublished)				
Walleye				
Lake Oahe (n = 15)	0.00–0.57	0.276	0.145	0.06–0.48
Lake Sakakawea (n = 15)	0.06–0.64	0.348	0.145	0.18–0.72
Merritt Reservoir (n = 15)	0.01–0.44	0.224	0.106	0.06–0.42
Combined	0.00–0.56	0.283	0.141	0.06–0.72

from Lake Oahe, South Dakota; Lake Sakakawea, North Dakota; and Merritt Reservoir, Nebraska (Table 1). Heparinized 10-ml syringes and 21-gauge needles were used to collect blood from live adult walleye by cardiac puncture. Samples were coagulated, clot-milked, and centrifuged within 24 hrs of collection. Sera were collected in microcentrifuge tubes, frozen on dry ice for transport to the laboratory, and placed in a −80 C freezer until analyzed.

Sigma Diagnostics (1989) protocol for the colorimetric determination of creatinine was utilized. A Bausch and Lomb Spectronic 20 was used to make determinations at 500 nm. Creatinine concentration in mg/dl was calculated using the manufacturer's formula, and dilutions of creatinine standard (15 mg/dl) were utilized as controls [illegible] procedures were reliable.

RESULTS AND DISCUSSION

Creatinine values from each lake were analyzed for normality using the Kolmogorov-Smirnov test (Sokal and Rohlf 1981). Data from each lake and pooled data were normally distributed since all "D" values were not significant ($p < .01$). Means were compared using Williams's (1974) modification of Tukey's Honestly Significant Difference test, and no significant differences occurred among values for each reservoir ($p < .01$).

Creatinine levels of walleye blood serum were within the range of values observed for other fish, e.g., *Salvelinus fontinalis* (brook trout), *Salmo trutta* (brown trout), *Oncorhynchus mykiss* (rainbow trout), *Cyprinus carpio* (carp), and *Ictalurus punctatus* (channel catfish;

Table 1). Mean creatinine concentration in walleye closely approximated the value for channel catfish (Warner and Williams 1977; Table 1). Besides specificity and ecology of the target population, the method of capture, age of fish, method of drawing blood, and diet are all variables that should be considered in accepting study specimens and evaluating results. However, Bentinck-Smith et al. (1987) suggested the variation in serum constituents in channel catfish was due principally to variability among individual fish. They contend that individual studies generate results characteristic of the species being analyzed and conditions to which the fish had been exposed. The 300% difference between the two channel catfish studies (Table 1) is too great to be explained by improved methodology and instrumentation in such a short time span. Thus, differences must be attributed to variation in channel catfish or inconsistencies in procedures. Walleye values may be useful as reference points in studies using similar fish-collecting, blood-sampling, and analysis methods in assessing the health of this species.

Circulating levels of creatinine are used primarily as an index of renal function in man (Hepler 1977). High serum creatinine concentrations are encountered in cases of human renal inflammation and obstruction, in some instances reflecting the degree of impairment. Smith (1929) showed creatinine to be excreted in the urine of fish. Thus, creatinine concentrations may be elevated in fish with diseases affecting the kidney (e.g., bacterial kidney disease). There was no apparent pathological evidence that the kidneys were diseased in fish examined.

Bentinck-Smith et al. (1987) stated that the analytical procedure utilized must be appropriate for each constituent being measured and that measurements must fall within the range of analytical linearity. When absorbance of diluted standards (0–10 mg/dl) was graphed (creatinine concentration on x-axis and absorbance on the y-axis), a straight line resulted. The reference values presented for creatinine in walleye blood serum meet these requirements and are of value in establishing a range of health. We consider creatinine values of 0.06–0.72 mg/dl (Table 1) representative of feral walleye populations sampled under field conditions and exhibiting no apparent disease symptoms or gross pathology. The levels reported for walleye are much higher (2–5 times) than for other species, except the more recent catfish study. We assume these differences to be due to development of more sensitive procedures and higher chemical specificity.

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INFLUENCE OF PREY MOVEMENT ON THE AIM OF PREDATORY STRIKES OF THE WESTERN RATTLESNAKE (*CROTALUS VIRIDIS*)

Douglas F. Schmidt[1, 2], William K. Hayes[1, 3], and Floyd E. Hayes[1, 4]

ABSTRACT—The purpose of this study was to determine whether the western rattlesnake (*Crotalus viridis*) aims its predatory strike at the head/thorax region of mice primarily on the basis of cues related to direction of prey movement. We hypothesized that when rattlesnakes strike at anesthetized, backward-moving mice, most strikes would be aimed at the forward-most-moving region, i.e., the posterior (abdomen/tail) region of prey. However, most mice were struck in the anterior (head/thorax) region, implying that the visual-infrared image of mice, rather than directional movement, guides the aim of predatory strikes.

Key words: Reptilia, Serpentes, rattlesnake, Crotalus viridis, *predator-prey, feeding behavior, strike aim.*

Rattlesnakes generally strike rodent prey in the head/thorax region (Minton 1969, Kardong 1986a, Hayes 1986, 1991, 1992a, Kardong and Mackessy 1991), which presumably reduces the risk of missing forward-moving prey (Hayes and Galusha 1984), provides the quickest means of prey death (Kardong 1986a, Hayes 1992a), and minimizes the threat of retaliatory injury inflicted by the rodent (Kardong 1986a, Hayes 1992b). Other ophidians that reportedly strike the head/thorax region of mice include the rat snakes *Elaphe climacophora* (Diefenbach and Emslie 1971) and *E. quadrivirgata* (Mori 1991) and the cottonmouth (*Agkistrodon piscivorus*) (Kardong 1982). The rough green snake (*Opheodrys aestivus*) also frequently strikes the anterior region of insects (Goldsmith 1986). However, when feeding on lizards, *E. quadrivirgata* and the Puerto Rican racer (*Alsophis portoricensis*) most often strike at the midbody (Mori 1991, Rodriguez-Robles 1992).

To aim the strike at the head/thorax region of a mouse, a rattlesnake must be able to differentiate the anterior and posterior ends (i.e., longitudinal "polarity") of potential prey. Discrimination of these regions may be accomplished by several means, including the visual and/or infrared image of the rodent (i.e., gross morphological features detected by the eyes and facial pits, respectively) and the direction of prey movement (Kardong 1986a, Kardong and Mackessy 1991). Based on photographic studies, Dieffenbach and Emslie (1971) suggested that movement of the mouse's head attracts the strike of *E. climacophora* to the anterior region. Hayes (1986), using featureless, cylindrical models of mice, concluded that direction of movement alone can be utilized by rattlesnakes to aim the strike at the forward-most-moving (anterior) region. Release of the predatory strike itself appears dependent upon prey movement (detected by visual and/or infrared cues; Chiszar et al. 1983, Hayes and Duvall 1991), since motionless, anesthetized, and dead mice, with all other stimuli present, often are not struck (Klauber 1956, Dullemeijer 1961, Cock Buning et al. 1981, Chiszar et al. 1992).

Thus, considering the significant contribution of prey movement to the predatory strike, we designed a test of our hypothesis that the western rattlesnake, *Crotalus viridis*, aims its strike primarily on the basis of cues related to direction of prey movement.

METHODS

Subjects were 14 adult northern Pacific rattlesnakes (*Crotalus viridis oreganus*) from southeastern Washington and two Great Basin rattlesnakes (*C. v. lutosus*) from southeastern

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[illegible] (*Mus musculus*) [illegible] and latency [illegible]. Mice [illegible] monofilament [illegible] forward or backward [illegible].

Direction of movement	Number of strikes[a]		Latency to strike[b]	
	Anterior	Posterior	$\bar{X}$	SD
Forward	9	5	56.0	52.2
Backward	10	5	47.0	49.9

[illegible]

Oregon. All were well habituated to captivity (1–3 years) and maintained on a 12:12 L:D cycle at 25–35 C. Prior to the study the snakes consumed live adult laboratory mice (*Mus musculus*) on an irregular (1–2/month) basis.

Our experimental design was to present rattlesnakes with anesthetized mice moving either forward or backward. The forward-moving mice served as controls, since we expected most strikes to be aimed at the anterior (head/thorax) region of the body (Kardong 1986a). For the backward-moving mice, we hypothesized that most strikes would be aimed at the forward-most-moving region, i.e., the posterior (abdomen/tail) region of the prey.

For each trial a snake was transferred to a 91 × 61 × 46-cm (L × W × H) wooden box. Adult laboratory mice were anesthetized with 0.1 mg Vetalar/g mouse, and a monofilament fishing line was tied around the center of the body to manipulate direction of mouse movement during presentation to the snake. Each snake was randomly assigned several forward- or backward-moving presentations, with a minimum of one day between successive trials. We assumed all strikes from a given snake were independent; no individual accounted for more than 20% of the data (cf. Kardong 1986a). Snakes were not allowed to consume struck mice until after completion of the study. Mice were dragged for several minutes in broad sweeps, at a 90° angle to the snake (Minton 1969), to within 15 cm of the snake's snout. Velocity of the moving mouse, determined from slow-motion videotape review, was approximately 50–150 cm/sec, which was comparable to sprint speeds of wild mice (*Peromyscus maniculatus*) measured by similar methods. For each presentation in which the [illegible] struck, a given mouse was used until [illegible] recorded the site on the mouse, either anterior or posterior half, where the fangs penetrated. Two mice struck exactly in the middle were discarded for the present purpose. Videotapes were made of most trials to confirm the accuracy of our observations and to measure the time (sec) until a strike was initiated; however, the sample of videotaped trials was reduced due to a malfunction of the video system. In agreement with Kardong (1982, 1986a), visual observations were sufficiently reliable for judging the site struck by the snakes.

Statistical tests, with alpha set at .05, followed Siegel (1956).

RESULTS

Data in Table 1 present the number of strikes delivered to the anterior and posterior halves of the anesthetized mice. No difference existed between forward-moving and backward-moving conditions (Table 1); mice were most often struck in the anterior (head/thorax) region regardless of the direction of movement. When data were pooled to include both forward- and backward-moving presentations, the proportion of mice bitten in the head/thorax region was significant (66% of all observations; one-tailed chi-square = 2.79, d.f. = 1, $p < .05$). From the videotaped trials, there also was no difference in latency to strike forward- ($n = 6$) or backward- ($n = 7$) moving mice (Table 1). Thus, the rattlesnakes treated forward- and backward-moving mice in a similar manner.

Field-by-field videotape analyses indicated the total duration of successful strikes ranged from 0.267 to 0.567 sec ($\bar{x} = 0.4$ sec); latency to contact the mouse was 0.067–0.333 sec, contact with the mouse lasted 0.067–0.167 sec, and recoil required 0.067–0.167 sec (cf. Van Riper 1955, Kardong 1986a, Rowe and Owings 1990, Hayes 1991, 1992a). There were no obvious differences in the form or success of strikes at forward- and backward-moving mice.

DISCUSSION

Although rattlesnakes apparently can utilize directional movement to aim the strike at the head/thorax region of mouse models (Hayes 1986), our results (Table 1) indicate that, when striking at live mice, the aim is guided primarily by other cues. Since the snakes mostly struck at the anterior (head/thorax) region of backward-moving mice, it seems likely that rattlesnakes discriminate the anterior and posterior ends of prey (i.e., longitudinal polarity) by visual and/or infrared cues rather than by directional movement. This conclusion is in disagreement with our original working hypothesis.

Although the relative contribution of visual and infrared cues remains unknown, the head/thorax-oriented strikes observed in a congenitally blind rattlesnake by Kardong and Mackessy (1991) suggest that polarity of the infrared image alone can be deciphered. However, Cock Buning et al. (1981) observed that blindfolded *Agkistrodon blomhoffi* occasionally strike the warm spot (an infrared cue) left behind when a mouse moves just before the strike, and suggested that visual cues may be relied on for aiming the strike. Considering the neural integration of the visual and infrared systems of rattlesnakes (Hartline 1984), it is likely that both systems, when functional, contribute to coordination of the strike aim.

From the slow-motion videotape analyses, it appeared that most strikes showed no deviation from their original course (cf. Kardong 1986b). Thus, we believe strikes delivered to anterior regions of moving prey were aimed on the basis of information received prior to striking. Accordingly, we concur with Kardong (1986a) and Kardong and Mackessy (1991) that rattlesnakes rely on visual and/or infrared cues to distinguish the most vulnerable (head/thorax) region of mice prior to the attack and aim their strike accordingly.

Although rattlesnakes typically aim their strike at the anterior region of mice, the reaction of the prey may limit their success. When striking at unrestrained lab mice (Kardong 1986a) and at items manipulated by monofilament line (anesthetized lab mice in this study and models of mice in Hayes 1986), snakes most frequently bite the head/thorax region. However, Hayes (1992a) found that strikes by prairie rattlesnakes (*C. v. viridis*) were distributed randomly along the axis of wild mice (*Peromyscus maniculatus*). The discrepancy is best explained by relative differences in mobility. Lab mice are much slower (Hayes and Galusha 1984) and undoubtedly less able to evade strikes than wild mice. Slow-motion videotape analyses indicate that the latter can often leap clear of the strike after it is launched by a snake (Hayes 1991, 1992a). Thus, a distinction can be made between what the snake aims at and where the fangs successfully contact prey.

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1993 UPDATE, CHECKLIST OF THE VASCULAR PLANTS OF BRYCE CANYON NATIONAL PARK, UTAH

John R. Spence[1] and Hayle Buchanan[2]

Abstract.—An updated checklist of the vascular flora of Bryce Canyon National Park is presented, including 458 species arranged in 232 genera and 73 families. Four species have been added to the park list based on 1991 fieldwork: *Arabis perennans*, *Arceuthobium divaricatum*, *Gentiana parryi*, and *Haplopappus acaulis*. Recent changes in nomenclature have been included, and several species identifications have been corrected. The six largest families are, in decreasing size, Asteraceace, Pocaceae, Fabaceae, Brassicaceae, Scrophulariaceae, and Rosaceae. Common names and an index are provided.

Key words: Bryce Canyon National Park, flora, vascular plants.

Recent fieldwork in Bryce Canyon National Park, along with nomenclatural changes in the Utah flora, has necessitated an updated version of the flora of Bryce Canyon National Park, south central Utah. The last published version of this species list is now 12 years old (Buchanan and Graybosch 1981). We offer this revised list hoping it will be useful to researchers currently engaged in vegetation and floristic work in and around the park.

Nomenclature in general follows the Intermountain Flora (Cronquist et al. 1972–1990), except for the substitution of the more recent treatment of the Poaceae in Arnow (1987). For those families not yet treated, Welsh et al. (1987) is used. We differ from the above volumes in the delimitation of some families. In particular, we cannot accept the outmoded use of the Polypodiaceae as a "catch-all" group for the ferns, as fern phylogeny has become increasingly stable over the last few years, and well-established classifications currently exist. We follow Weber (1987), who has provided an analysis of the new classification for regional ferns. Only two genera occur at Bryce Canyon, *Cheilanthes*, in the Sinopteridaceae, and *Pteridium*, in the Hypolepidaceae. We also follow the now well-established classification for the Liliaceae and its allies, which has become generally accepted worldwide (Dahlgren et al. 1985). Hence, in addition to the Liliaceae, we have members of the Agavaceae, Alliaceae, Asparagaceae, Calochortaceae, Convallariaceae, and Melanthiaceae in the park flora. Although we feel that the alternative classifications of Weber (1987) have much to offer, we think it premature to utilize his system in its entirety, as this would

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necessitate numerous nomenclatural innovations for Utah taxa. Hence, only three genera are accepted that differ from the treatments in A Utah Flora and Intermountain Flora: *Bistorta* (*Polygonum* in part), *Ipomopsis* (*Gilia* in part), and *Pseudocymopterus* (*Cymopterus* in part). We utilize these because they have been widely accepted in North American floristic work. Finally, we note that there are fundamental differences in nomenclature at the species level for some plants at Bryce Canyon when Welsh et al. (1987) and Weber (1987) are compared; e.g., in *Arabis*, *Euphorbia*, *Solidago*, and *Stephanomeria* among others. We hope that future revisionary work on these taxa will resolve these nomenclatural differences.

We have incorporated the additions to the park flora made by Hallsten and Roberts (1988). Also, four species have been added to the 1981 list based on recent fieldwork and corrections of herbarium material: *Arabis perennans*, *Arceuthobium divaricatum*, *Gentiana parryi*, and *Haplopappus acaulis* (Spence 1992). Several species have either been dropped from the list or replaced by other species, based on misidentifications or changes in our understanding of the taxonomy and distributions of certain taxa in Utah. These are listed in Table 1. The Atlas of the Vascular Plants of Utah (Albee et al. 1988) was consulted for range information. If a species on the 1981 list was not represented in the park herbarium, and was well outside its normal range in Utah based on the atlas, it was excluded. The checklist that follows is organized alphabetically by family, genus, and species.

Table 2 includes a list of species that have been found around the boundaries of Bryce Canyon National Park but are not yet known from within the park. Future fieldwork is likely to find some of these species in the park.

CHECKLIST OF THE VASCULAR PLANTS OF BRYCE CANYON NATIONAL PARK

ACERACEAE

1. *Acer glabrum* Torr.	Rocky Mountain maple
2. *A. grandidentatum* Nutt.	bigtooth maple

AGAVACEAE

3. *Yucca angustissima* Trel.	narrowleaf yucca
4. *Y. harrimaniae* Trel.	Harriman yucca

ALLIACEAE

5. *Allium acuminatum* Hook.	tapertip onion
6. *A. nevadense* S. Wats.	Nevada onion

AMARANTHACEAE

7. *Amaranthus blitoides* Wats.	prostrate pigweed

ANACARDIACEAE

8. *Rhus trilobata* Nutt.	squawbush

APIACEAE

9. *Berula erecta* (Huds.) Cov.	cutleaf waterparsnip
10. *Cicuta maculata* L.	water hemlock
11. *Cymopterus purpureus* Wats.	purple springparsley
12. *Ligusticum porteri* Coult. & Rose	southern ligusticum
13. *Lomatium minimum* (Math.) Math.	least biscuitroot

TABLE 1. Changes in species identifications in, and deletions from, the 1981 list of the flora of Bryce Canyon National Park. 1 = outside range, misidentification, deleted from list; 2 = inside range, misidentification, retained in list.

Taxa previously reported	Current justification and status
Arenaria nuttallii Pax	(1) no specimen, outside range
Campanula rotundifolia L.	(2) *C. parryi* Gray
[illegible] Greene	(2) *E. compositus* Pursh
[illegible] Keith	(2) *G. tortuosa* (Jones) J. Gillett
[illegible] (Gray) Macbr.	(2) *L. parryi* (Wats.) Macbr.
[illegible] (Gray) [illegible] Nels.	(2) *P. pulvinata* (Wherry) Cronq.
[illegible]	(2) *P. hoodii* Richards
[illegible]	(2) *P. pulvinata* (Wherry) Cronq.
Phy[illegible]	(1) no specimen, outside range
Pole[illegible]	(1) no specimen, outside range
Scirpus [illegible]	(2) *S. pungens* Vahl
Senecio [illegible]	(2) *S. hartianus* Heller
Solidago occi[illegible]	(2) *S. sparsiflora* Gray
Tanacetum nutta[illegible]	(2) *Sphaeromeria capitata* Nutt.
Thelypodium sagittatu[illegible]	(1) no specimen, outside range

Table 2. List of species reported from near the boundary of Bryce Canyon National Park, but not yet collected from within the park.

Asclepiadaceae
- *Asclepias cryptoceras* Wats.

Asteraceae
- *Artemisia filifolia* Torr.
- *Cirsium clavatum* (Jones) Petrak
- *C. wheeleri* (Gray) Petrak
- *Crepis atrabarba* Heller
- *Erigeron aphanactis* (Gray) Greene
- *E. lonchophyllus* Hook.
- *Haplopappus lanceolatus* Hook.
- *H. parryi* Gray
- *Hymenoxys depressa* (T. & G.) Welsh & Reveal
- *Senecio canus* Hook.
- *Solidago nana* Nutt.
- *Stephanomeria exigua* Nutt.

Brassicaceae
- *Arabis drummondii* Gray
- *Lepidium lasiocarpum* Nutt.
- *Lesquerella wardii* Wats.
- *Thlaspi montanum* L.

Caprifoliaceae
- *Sambucus racemosa* L.

Cyperaceae
- *Carex egglestonii* Mack.
- *C. petasata* Dewey
- *C. simulata* Mack.

Ephedraceae
- *Ephedra viridis*

Fabaceae
- *Astragalus lentiginosus* Hook.
- *A. wardii* Gray
- *Trifolium kingii* Wats.

Grossulariaceae
- *Ribes montigenum* McClat.

Hypericaceae
- *Hypericum formosum* H.B.K.

Iridaceae
- *Sisyrinchium idahoense* Bickn.

Juncaceae
- *Juncus mertensianus* Bong.

Lamiaceae
- *Mentha arvensis* L.

Linaceae
- *Linum australe* Heller

Orchidaceae
- *Habenaria hyperborea* (L.) R.Br.

Pinaceae
- *Abies lasiocarpa* (Hook.) Nutt.
- *Picea engelmannii* Engelm.

Poaceae
- *Lolium perenne* L.

Polemoniaceae
- *Leptodactylon caepitosum* Nutt.

Polygonaceae
- *Eriogonum arctioides* Barneby

Ranunculaceae
- *Caltha leptosepala* DC.

Rosaceae
- *Amelanchier alnifolia* Nutt.
- *Ivesia kingii* Wats.

Salicaceae
- *Salix boothii* Dorn

Scrophulariaceae
- *Cordylanthus wrightii* Gray
- *Pedicularis groenlandica* Retz.
- *Penstemon laevis* Pennell
- *P. procerus* Graham

Solanaceae
- *Datura stramonium* L.
- *Nicotiana attenuata* Wats.

Sparganiaceae
- *Sparganium eurycarpum* Engelm.

Violaceae
- *Viola nephrophylla* Greene

14. *L. parryi* (Wats.) Macbr.	Parry biscuitroot
15. *Pseudocymopterus montanus* (Gray) Coult. & Rose	mountain parsley
Apocynaceae	
16. *Apocynum androsaemifolium* L.	spreading dogbane
Asclepiadaceae	
17. *Asclepias asperula* (Dcne.) Woodson	spider milkweed
18. *A. speciosa* Torr.	showy or common milkweed
Asparagaceae	
19. *Asparagus officinalis* L.	asparagus
Asteraceae	
20. *Achillea lanulosa* Nutt.	yarrow
21. *Agoseris aurantiaca* (Hook.) Greene	orange agoseris

[illegible]	
var. [illegible] (Gray) Greene	
22. *Agoseris glauca* (Pursh) D. Dietr.	mountain dandelion
var. *parviflora* (Nutt.) Rydb.	
23. *Antennaria dimorpha* (Nutt.) T. & G.	low pussytoes
24. *A. microphylla* Rydb.	rosy pussytoes
25. *A. parvifolia* Nutt.	small-leaf pussytoes
26. *A. rosulata* Rydb.	woolly pussytoes
27. *Arnica chamissonis* Less.	Chamisso arnica
28. *A. cordifolia* Hook.	heartleaf arnica
29. *Artemisia campestris* L.	field sagewort
30. *A. carruthii* Wood ex Carruth	Carruth sagewort
31. *A. dracunculus* L.	tarragon
32. *A. frigida* Willd.	fringed sagewort
33. *A. ludoviciana* Nutt.	foothill sagebrush
34. *A. nova* A. Nels.	black sagebrush
35. *A. pygmaea* Gray	pigmy sagebrush
36. *A. tridentata* Nutt.	big sagebrush
37. *Aster chilensis* Nees	Pacific aster
38. *A. eatonii* (Gray) Howell	Eaton aster
39. *A. glaucodes* Blake	blueleaf aster
40. *A. occidentalis* (Nutt.) Torr. & Gray	western aster
41. *Balsamorhiza sagittata* (Pursh) Nutt.	arrowleaf balsamroot
42. *Brickellia oblongifolia* Nutt.	Mojave brickellbush
43. *Centaurea repens* L.	Russian knapweed
44. *Chaenactis douglasii* (Hook.) H. & A.	Douglas dustymaiden
45. *Chrysothamnus depressus* Nutt.	dwarf rabbitbrush
46. *C. linifolius* Greene	spreading rabbitbrush
47. *C. nauseosus* (Pallas) Britt.	rubber rabbitbrush
var. *glabratus* (Gray) Cronq.	
48. *C. parryi* (Gray) Greene	Parry rabbitbrush
49. *C. vaseyi* (Gray) Greene	Vasey rabbitbrush
50. *C. viscidiflorus* (Hook.) Nutt.	mountain rabbitbrush
51. *Cirsium arizonicum* (Gray) Petrak	Arizona thistle
var. *arizonicum*	
var. *nidulum* (Jones) Welsh	
52. *C. calcareum* (Jones) Woot. & Standl.	limestone thistle
var. *pulchellum* (Greene) Welsh	
53. *C. neomexicanum* Gray	New Mexico thistle
54. *C. undulatum* (Nutt.) Sprengel	wavyleaf thistle
55. *C. vulgare* (Savi) Ten.	bull thistle
56. *Conyza canadensis* (L.) Cronq.	Canada horseweed
57. *Crepis intermedia* Gray	Gray hawksbeard
58. *C. occidentalis* Nutt.	western hawksbeard
59. *C. runcinata* (James) T. & G.	meadow hawksbeard
var. *glauca* (Nutt.) Babcock & Stebbins	
60. *Erigeron abajoensis* Cronq.	Abajo fleabane
61. *E. canus* Gray	hoary fleabane
62. *E. compositus* [illegible]	fernleaf fleabane
63. *E. divergens* T. & [illegible]	spreading fleabane
64. *E. eatonii* Gray	Eaton fleabane
65. *E. flagellaris* Gray	trailing fleabane
66. *E. pumilus* Nutt.	low fleabane
ssp. *concinnoides* Cronq.	
67. *E. speciosus* (Lindl.) DC.	Oregon fleabane
68. *E. ursinus* D.C. Eaton	bear fleabane
69. *E. vagus* Payson	wandering fleabane
70. *Grindelia squarrosa* (Pursh) Dunal	curlycup gumweed
71. *Gutierrezia sarothrae* (Pursh) Britt. & Rusby	broom snakeweed
72. *Haplopappus acaulis* (Nutt.) Gray	stemless goldenweed
73. *H. armerioides* (Nutt.) Gray	thrifty goldenweed
74. *H. scopulorum* (Jones) Blake	Rocky Mountain goldenweed
75. *H. zionis* L.C. Anderson	Cedar Breaks goldenweed
76. *Helianthella uniflora* (Nutt.) T. & G.	little sunflower
77. *Helianthus annuus* L.	common sunflower
78. *Heliomeris multiflora* Nutt.	showy goldeneye
79. *Heterotheca jonesii* (Blake) Welsh & Atwood	Jones goldenaster
80. *H. villosa* (Pursh) Shinn.	hoary goldenaster
81. *Hymenopappus filifolius* Hook.	hymenopappus
var. *cinereus*	
var. *lugens* (Greene) Jeps.	
82. *Hymenoxys acaulis* (Pursh) Parker	stemless woollybase
83. *H. richardsonii* (Hook.) Cockerell	Colorado rubberplant
84. *Iva axillaris* Pursh	poverty sumpweed
85. *Lactuca serriola* L.	prickly lettuce
86. *L. taractica* (L.) C.A. May	blue lettuce
spp. *pulchella* (Pursh) Stebbins	
87. *Leucelene ericoides* (Torr.) Greene	rose heath
88. *Lygodesmia grandiflora* (Nutt.) T. & G.	showy rushpink
89. *Machaeranthera canescens* (Pursh) Gray	hoary tansyaster
90. *M. grindelioides* (Nutt.) Shinners	gumweed tansyaster
91. *M. linearis* Greene	tansy aster
92. *Petradoria pumila* (Nutt.) Greene	rock goldenrod
93. *Senecio atratus* Greene	black groundsel
94. *S. hartianus* Heller	Hart groundsel
95. *S. hydrophilus* Nutt.	water groundsel
96. *S. multilobatus* T. & G.	Uintah groundsel
97. *S. spartioides* T. & G.	broom groundsel
98. *Solidago spathulata* DC.	coast goldenrod
99. *S. parryi* (Gray) Greene	Parry goldenrod
100. *S. sparsiflora* Gray	few-flowered goldenrod
101. *Sphaeromeria capitata* Nutt.	sphaeromeria

102. *Stephanomeria spinosa* (Nutt.) Tomb	thorn wirelettuce
103. *S. tenuifolia* (Torr.) Hall	slenderleaf wirelettuce
104. *Taraxacum officinale* Weber	common dandelion
105. *Tetradymia canescens* DC.	Gray horsebrush
106. *Townsendia exscapa* (Richards) Porter	stemless townsendia
107. *T. incana* Nutt.	hoary townsendia
108. *T. minima* Eastw.	least townsendia
109. *Tragopogon dubius* Scop.	yellow salsify
110. *Verbesina encelioides* (Cav.) Benth. & Hook.	golden crownbeard

BERBERIDACEAE

111. *Mahonia fremontii* (Torr.) Fedde	Fremont mahonia
112. *M. repens* (Lindl.) G. Don	Oregon grape

BETULACEAE

113. *Betula occidentalis* Hook.	western water birch

BORAGINACEAE

114. *Cryptantha abata* I.M. Johnston	low cryptanth
115. *C. bakeri* (Greene) Payson	Baker cryptanth
116. *C. confertifolia* (Greene) Payson	golden cryptanth
117. *C. fendleri* (Gray) Greene	sand dune cryptanth
118. *C. flava* (Nels.) Payson	yellow cryptanth
119. *C. fulvocanescens* (Gray) Payson	plateau cryptanth
120. *C. humilus* (Greene) Payson	roundspike cryptanth
121. *C. jamesii* (Torr.) Payson	James cryptanth
122. *C. ochroleuca* Higgins	yellowish cryptanth
123. *C. setosissima* (Gray) Payson	bristly cryptanth
124. *Lappula occidentalis* (Wats.) Greene	western stickseed
125. *Lithospermum incisum* Lehm.	showy stickseed
126. *L. multiflorum* Torr.	southwestern stickseed
127. *Mertensia arizonica* Greene	aspen bluebell

BRASSICACEAE

128. *Arabis demissa* Greene	rockcress
129. *A. holboellii* Hornem. var. *fendleri* Wats. var. *holboellii*	Holboell rockcress
130. *A. perennans* Wats.	common rockcress
131. *Capsella bursa-pastoris* (L.) Medic	shepherd's purse
132. *Caulanthus crassicaulis* (Torr.) S. Wats.	thickstem wildcabbage
133. *Conringia orientalis* (L.) Dumort	hare's ear mustard
134. *Descurainia richardsonii* (Sweet) O.E. Schulz	Richardson tansymustard
135. *D. sophia* (L.) Webb	flixweed
136. *Draba subalpina* Goodman & Hitchc.	breaks draba
137. *Erysimum asperum* (Nutt.) DC.	western wallflower
138. *E. inconspicuum* (S. Wats.) MacMill	small wallflower
139. *Lepidium densiflorum* Schrad.	prairie pepperweed
140. *L. montanum* Nutt.	mountain pepperweed
141. *Lesquerella intermedia* (S. Wats.) Heller	Watson bladderpod
142. *L. kingii* S. Wats. var. *parvifolia* (Maguire & Holmgren) Welsh & Reveal	King bladderpod
143. *L. rubicundula* Rollins	breaks bladderpod
144. *Malcolmia africana* (L.) R. Br.	African mustard
145. *Physaria chambersii* Rollins	Chamber twinpod
146. *P. newberryi* Gray	Newberry twinpod
147. *Schoencrambe linifolia* (Nutt.) Greene	schoencrambe
148. *Stanleya pinnata* (Pursh) Britton	prince's plume
149. *Streptanthus cordatus* Nutt.	twistflower
150. *Thelypodium sagittatum* (Nutt.) Endl. var. *ovalifolium* (Rydb.) Welsh & Reveal	arrowleaf thelypody
151. *Thlaspi arvense* L.	field pennycress

CACTACEAE

152. *Echinocereus triglochidiatus* Engelm.	claret cup
153. *Opuntia erinacea* Engelm. & Bigel.	grizzlybear pricklypear
154. *Pediocactus simpsonii* (Engelm.) Britt. & Rose	Simpson pediocactus
155. *Sclerocactus whipplei* (Engelmn. & Bigel.) Britt. & Rose	fishhook cactus

CALOCHORTACEAE

156. *Calochortus nuttallii* T. & G.	sego lily

CAMPANULACEAE

157. *Campanula parryi* Gray	Parry bellflower

CAPPARACEAE

158. *Cleome lutea* Hook.	yellow beeplant

CAPRIFOLIACEAE

159. *Sambucus cerulea* Raf.	blue elderberry
160. *Symphoricarpos oreophilus* Gray	mountain snowberry

CARYOPHYLLACEAE

161. *Arenaria fendleri* A. Gray	Fendler sandwort
162. *Lychnis drummondii* (Hook.) S. Wats.	Drummond catchfly

163. [illegible] Nutt.	creeping nailwort
164. *Silene petersonii* Maguire var. *minor* C. L. Hitchc. & Maguire	Peterson campion
165. *Stellaria jamesiana* Torr.	James chickweed
166. *S. longipes* Goldie	longstalk chickweed

CELASTRACEAE

167. *Paxistima myrsinites* (Pursh) Raf.	mountain lover

CHENOPODIACEAE

168. *Atriplex canescens* (Pursh) Nutt.	fourwing saltbush
169. *A. confertifolia* (Torr. & Frem.) Wats.	shadscale
170. *A. gardneri* (Moq.) D. Dietr. var. *tridentata* (Kuntze) MacBr.	Gardner saltbush
171. *Chenopodium atrovirens* Rydb.	mountain goosefoot
172. *C. fremontii* Wats. var. *incanum* Wats.	Fremont goosefoot
173. *C. leptophyllum* Nutt.	narrowleaf goosefoot
174. *Eurotia lanata* (Pursh) Moq.	winterfat
175. *Salsola iberica* Sennen & Pau	Russian thistle
176. *Sarcobatus vermiculatus* (Hook.) Torr.	greasewood

CONVALLARIACEAE

177. *Smilacina stellata* (L.) Desf.	starry false Solomon seal

CONVOLVULACEAE

178. *Convolvulus arvensis* L.	field bindweed

CORNACEAE

179. *Cornus stolonifera* Michx.	red-osier dogwood

CUPRESSACEAE

180. *Juniperus communis* L.	common juniper
181. *J. osteosperma* (Torr.) Little	Utah juniper
182. *J. scopulorum* Sarg.	Rocky Mountain juniper

CYPERACEAE

183. *Carex athrostachya* [illegible]	slenderbeak sedge
184. *C.* [illegible]	golden sedge
185. *C.* [illegible]	pale sedge
186. *C.* [illegible]	Douglas sedge
187. *C.* [illegible]	smallwing sedge
188. *C. ne*[illegible]	Nebraska sedge
189. *C. oederi* [illegible]	green sedge
190. *C. praegraci*[illegible]	[illegible] sedge
191. *C. rossii* F. Boott	Ross sedge
192. *C. rostrata* Stokes	beaked sedge
193. *C. stenophylla* Wahl.	narrowleaf sedge
194. *Eleocharis palustris* (L.) R. & S.	common spikerush
195. *E. pauciflorus* (Lightf.) Link	spikerush
196. *E. rostellata* (Torr.) Torr.	beaked spikerush
197. *Scirpus pungens* Pers.	common threesquare bulrush

ELAEAGNACEAE

198. *Shepherdia argentea* (Pursh) Nutt.	silver buffaloberry
199. *S. canadensis* (L.) Nutt.	russet buffaloberry
200. *S. rotundifolia* Parry	roundleaf buffaloberry

EQUISETACEAE

201. *Equisetum arvense* L.	field horsetail
202. *E. laevigatum* A. Br.	smooth horsetail

ERICACEAE

203. *Arctostaphylos patula* Greene	greenleaf manzanita
204. *A. uva-ursi* (L.) Spreng.	bearberry

EUPHORBIACEAE

205. *Euphorbia brachycera* Engelm.	shorthorn spurge
206. *E. fendleri* T. & G.	Fendler spurge

FABACEAE

207. *Astragalus agrestis* G. Don	field milkvetch
208. *A. amphioxys* Gray	crescent milkvetch
209. *A. argophyllus* T. & G.	silverleaf milkvetch
210. *A. bisulcatus* (Hook.) Gray	two-grooved milkvetch
211. *A. calycosus* Wats.	Torrey milkvetch
212. *A. convallarius* Greene	timber milkvetch
213. *A. hallii* Gray	Hall milkvetch
214. *A. humistratus* Gray	groundcover milkvetch
215. *A. kentrophyta* Gray	kentrophyta
216. *A. lonchocarpus* Torr.	great rushy milkvetch
217. *A. megacarpus* (Nutt.) Gray	great bladdery milkvetch
218. *A. miser* Hook.	weedy milkvetch
219. *A. tenellus* Pursh	pulse milkvetch
220. *Hedysarum boreale* Nutt.	northern sweetvetch
221. *Lathyrus brachycalyx* Rydb.	purple peavine
222. *Lotus utahensis* Ottley	Utah trefoil
223. *Lupinus argenteus* Pursh var. *argenteus* var. *rubricaulis* (Greene) Welsh	silvery lupine
224. *L. kingii* S. Wats.	King lupine
225. *L. sericeus* Pursh	silky lupine
226. *Medicago lupulina* L.	black medic
227. *M. sativa* L.	alfalfa

228. *Melilotus officinalis* (L.) Pall.	yellow sweetclover
229. *Oxytropis deflexa* (Pall.) DC. var. *sericea* T. & G.	hangpod locoweed
230. *O. oreophila* Gray	mountain locoweed
231. *Pediomelum pariense* (Welsh & Atwood) J. Grimes	Paria breadroot
232. *Trifolium repens* L.	white clover
233. *Vicia americana* Willd.	American vetch

Fagaceae

234. *Quercus gambelii* Nutt.	Gambel oak

Fumariaceae

235. *Corydalis aurea* Willd.	golden corydalis

Gentianaceae

236. *Frasera speciosa* Griseb.	elkweed
237. *Gentiana affinis* Griseb.	Rocky Mountain gentian
238. *G. parryi* Engelm.	Parry gentian
239. *Gentianella heterosepala* (Engelm.) Holub	Engelmann gentian
240. *G. tortuosa* (Jones) J. Gillett	Jones gentian
241. *Gentianopsis detonsa* (Rottb.) Ma	fringed gentian

Geraniaceae

242. *Geranium caespitosum* James	small-leaf geranium
243. *G. richardsonii* Fisch. & Trautv.	Richardson geranium

Grossulariaceae

244. *Ribes aureum* Pursh	golden currant
245. *Ribes cereum* Dougl.	wax or squaw currant

Hypolepidaceae

246. *Pteridium aquilinum* (L.) Kuhn	bracken fern

Iridaceae

247. *Iris missouriensis* Nutt.	Missouri iris
248. *Sisyrinchium demissum* Greene	blue-eyed grass

Juncaceae

249. *Juncus arcticus* Willd.	wiregrass
250. *J. bufonius* L.	toad rush
251. *J. ensifolius* Wikstr.	swordleaf rush
252. *J. longistylis* Torr.	longstyle rush
253. *J. torreyi* Coville	Torrey rush

Juncaginaceae

254. *Triglochin maritima* L.	maritime arrowgrass
255. *T. palustris* L.	marsh arrowgrass

Lamiaceae

256. *Dracocephalum parviflorum* Nutt.	American dragonhead
257. *Hedeoma drummondii* Benth.	mock pennyroyal
258. *Marrubium vulgare* L.	hoarhound
259. *Monardella odoratissima* Benth.	cloverhead horsemint
260. *Prunella vulgaris* L.	selfheal

Liliaceae

261. *Fritillaria atropurpurea* Nutt.	leopard lily
262. *Leucocrinum montanum* Nutt. ex Gray	star lily

Linaceae

263. *Linum aristatum* Engelm.	broom flax
264. *L. kingii* Wats.	King flax
265. *L. lewisii* Pursh	blue flax

Loasaceae

266. *Mentzelia multiflora* (Nutt.) Gray	desert blazing star

Malvaceae

267. *Sphaeralcea coccinea* (Pursh) Rydb.	scarlet globemallow
268. *S. parvifolia* A. Nels.	small-flowered globemallow

Melanthiaceae

269. *Zigadenus elegans* Pursh	mountain death camas

Nyctaginaceae

270. *Abronia fragrans* Hook.	fragrant sand verbena
271. *A. nana* Wats.	low sand verbena

Onagraceae

272. *Calylophus lavandulifolius* (T. & G.) Raven	lavender evening primrose
273. *Epilobium angustifolium* L.	fireweed
274. *E. ciliatum* Raf.	northern willowherb
275. *Gayophytum ramosissimum* T. & G.	branchy groundsmoke
276. *G. racemosum* T. & G.	kitchenweed
277. *Oenothera caespitosa* Nutt.	tufted evening primrose
278. *O. coronopifolia* T. & G.	rootstalk evening primrose
279. *O. flava* (A. Nels.) Garrett	yellow evening primrose
280. *O. howardii* (A. Nels.) W. L. Wagner	bronze evening primrose
281. *O. longissima* Rydb.	Bridges evening primrose

282. [illegible]	pale evening primrose

ORCHIDACEAE

283. Corallorhiza maculata Raf.	spotted coralroot
284. C. striata Lindl.	striped coralroot
285. *Epipactis gigantea* Dougl. ex Hook.	giant helleborine
286. *Habenaria dilatata* (Pursh) Hook.	white bog orchid
287. *H. sparsiflora* S. Wats.	Watson bog orchid

OROBANCHACEAE

288. *Orobanche fasciculata* Nutt.	clustered broomrape

PINACEAE

289. *Abies concolor* (Gord. & Glend.) Lindl.	white fir
290. *Picea pungens* Engelm.	blue spruce
291. *Pinus edulis* Engelm.	two-needle pinyon
292. *P. flexilis* James	limber pine
293. *P. longaeva* D. K. Bailey	bristlecone pine
294. *P. ponderosa* Laws.	ponderosa pine
295. *Pseudotsuga menziesii* (Mirb.) Franco	Douglas fir

PLANTAGINACEAE

296. *Plantago eriopoda* Torr.	woolly-foot plaintain
297. *P. lanceolata* L.	English plaintain

POACEAE

298. *Agropyron cristatum* (L.) Gaertn.	crested wheatgrass
299. *Agrostis stolonifera* L.	carpet bentgrass
300. *Aristida purpurea* Nutt.	purple threeawn
301. *Bouteloua gracilis* (H.B.K.) Lag. ex Steudel	blue grama
302. *Bromus anomalus* Rupr. ex Fourn.	nodding brome
303. *B. carinatus* H. & A.	mountain brome
304. *B. ciliatus* L.	fringed brome
305. *B. inermis* Leysser	smooth brome
306. *B. japonicus* Thunb. ex Murray	meadow brome
307. *B. tectorum* L.	cheatgrass
308. *Calamagrostis scopulorum* M.E. Jones	Jones reedgrass
309. *C.* [illegible] Koeler	slimstem reedgrass
310. *Dactylis* [illegible] L.	orchard grass
311. [illegible]	tufted hairgrass
312. *E*[illegible]	Canada wildrye
313. *E.* [illegible]	squirrel tail
314. *E.* [illegible]	blue wildrye
315. *E.* [illegible]	Russian wildrye
316. *E.* [illegible] & S[illegible]	thickspike wheatgrass
317. *E. salina*	Salina wildrye
318. *E. scribneri*	[illegible] wheatgrass
319. *E. smithii* (Rydb.) Gould	western wheatgrass
320. *E. spicatus* (Pursh) Gould	bluebunch wheatgrass
321. *E. trachycaulis* (Link) Gould ex Shinners	slender wheatgrass
322. *Festuca octoflora* Walter	six weeks fescue
323. *F. ovina* L.	sheep fescue
324. *F. pratensis* Hudson	meadow fescue
325. *Glyceria striata* (Lam.) A.S. Hitchc.	fowl mannagrass
326. *Hilaria jamesii* (Torr.) Benth.	galleta
327. *Hordeum brachyantherum* Nevski	meadow barley
328. *H. jubatum* L.	foxtail barley
329. *Koeleria macrantha* (Ledeb.) Schultes	Junegrass
330. *Muhlenbergia andina* (Nutt.) A.S. Hitchc.	foxtail muhly
331. *M. asperifolia* (Nees & Meyer) L.R. Parodi	scratchgrass
332. *M. montana* (Nutt.) A.S. Hitchc.	mountain muhly
333. *M. pungens* Thurber	sandhill muhly
334. *M. richardsonis* (Trin.) Rydb.	mat muhly
335. *Oryzopsis micrantha* (Trin. & Rupr.) Thurber	littleseed ricegrass
336. *Phleum pratense* L.	timothy
337. *Poa compressa* L.	Canada bluegrass
338. *P. fendleriana* (Steudel) Vasey	muttongrass
339. *P. pratensis* L.	Kentucky bluegrass
340. *P. reflexa* Vasey & Scribn.	nodding bluegrass
341. *P. secunda* Presl.	Sandberg bluegrass
342. *Puccinellia nuttalliana* (Schultes) A.S. Hitchc.	Nuttall alkaligrass
343. *Schizachyrium scoparium* (Michx.) Nash	little bluestem
344. *Sporobolus airoides* (Torr.) Torr.	alkali sacaton
345. *S. cryptandrus* (Torr.) Gray	sand dropseed
346. *Stipa comata* Trin. & Rupr.	needle-and-thread
347. *S. hymenoides* R. & S.	Indian ricegrass
348. *S. lettermanii* Vasey	Letterman needlegrass
349. *S. nelsonii* Scribn.	Nelson needlegrass
350. *S. pinetorum* Jones	pinewoods needlegrass

POLEMONIACEAE

351. *Ipomopsis aggregata* (Pursh) V. Grant	scarlet gilia, skyrocket
352. *I. congesta* (Hook.) V. Grant	ballhead gilia
353. *Leptodactylon pungens* (Torr.) Nutt.	prickly phlox
354. *Linanthastrum nuttallii* (Gray) Ewan	Nuttall flaxflower
355. *Phlox austromontana* Cov.	desert phlox
356. *P. hoodii* Richards.	carpet phlox
357. *P. longifolia* Nutt.	longleaf phlox
358. *P. muscoides* Nutt.	moss phlox

359. *P. pulvinata* (Wherry) Cronq.	cushion phlox
360. *Polemonium caeruleum* L.	western Jacobs ladder

Polygonaceae

361. *Bistorta vivipara* (L.) S. Gray	American bistort
362. *Eriogonum alatum* Torr.	winged buckwheat
363. *E. corymbosum* Benth.	Corymb buckwheat
364. *E. microthecum* Nutt. var. *foliosum* (T. & G.) Reveal	slender buckwheat
365. *E. panguicense* (M.E. Jones) Reveal	Panguitch buckwheat
366. *E. racemosum* Nutt.	redroot buckwheat
367. *E. subreniforme* S. Wats.	Stokes buckwheat
368. *E. umbellatum* Torr. var. *subaridum* Stokes	sulphur buckwheat
369. *Polygonum aviculare* L.	knotweed
370. *P. douglasii* Greene var. *johnstonii* Munz	Douglas knotweed
371. *P. ramosissimum* Michx.	bushy knotweed
372. *Rumex crispus* L.	curly dock
373. *R. salicifolius* Weinm. var. *triangulivalis* Danser.	beach dock

Primulaceae

374. *Androsace septentrionalis* L.	pygmy-flower rockjasmine
375. *Dodecatheon pulchellum* (Raf.) Merrill	pretty shooting star

Pyrolaceae

376. *Pyrola asarifolia* Michx.	liverleaf wintergreen
377. *P. virens* Schweigg.	green wintergreen
378. *Pterospora andromedea* Nutt.	pinedrops

Ranunculaceae

379. *Aconitum columbianum* Nutt.	monkshood
380. *Anemone multifida* Poir.	globeflower
381. *Aquilegia caerulea* James	Colorado columbine
382. *A. scopulorum* Tides.	rock columbine
383. *Clematis columbiana* (Nutt.) T. & G.	Rocky Mountain clematis
384. *C. ligusticifolia* Nutt.	white virgin's bower
385. *Delphinium andersonii* Gray var. *scaposum* (Greene) Welsh	Anderson larkspur
386. *Ranunculus cymbalaria* Pursh	marsh buttercup
387. *R. flammula* L.	spearwort
388. *R. inamoenus* Greene	drab buttercup
389. *Thalictrum fendleri* Engelm.	Fendler meadowrue

Rhamnaceae

390. *Ceanothus fendleri* Gray	Fendler mountain lilac
391. *C. martinii* M.E. Jones	Utah mountain lilac

Rosaceae

392. *Amelanchier utahensis* Koehne	Utah serviceberry
393. *Cercocarpus ledifolius* Nutt.	curlleaf mountain mahogany
394. *C. montanus* Raf.	alder leaf mountain mahogany
395. *Fallugia paradoxa* (D. Don) Endl.	Apache plume
396. *Fragaria virginiana* Duchesne	mountain strawberry
397. *Holodiscus dumosus* (Hook.) Heller	bush ocean spray
398. *Ivesia sabulosa* (M.E. Jones) Keck	Sevier ivesia
399. *Peraphyllum ramosissimum* Nutt.	squaw-apple
400. *Potentilla anserina* L.	silverweed cinquefoil
401. *P. concinna* Richards	pretty cinquefoil
402. *P. crinita* Gray	bearded cinquefoil
403. *P. fruticosa* L.	shrubby cinquefoil
404. *P. gracilis* Dougl. var. *pulcherrima* (Lehm.) Fern.	slender cinquefoil
405. *P. plattensis* Nutt.	cinquefoil
406. *Prunus virginiana* L.	chokecherry
407. *Purshia mexicana* (D. Don) Welsh	cliffrose
408. *P. tridentata* (Pursh) DC.	bitterbrush
409. *Rosa nutkana* Presl.	Nutka rose
410. *R. woodsii* Lindl.	Woods rose
411. *Rubus idaeus* L. var. *sachalinensis* (Levl.) Focke	raspberry

Rubiaceae

412. *Galium trifidum* L.	small bedstraw
413. *Kelloggia galioides* Torr.	kelloggia

Salicaceae

414. *Populus angustifolia* James	narrowleaf cottonwood
415. *P. fremontii* S. Wats.	Fremont cottonwood
416. *P. tremuloides* Michx.	quaking aspen
417. *Salix bebbiana* Sarg.	Bebb willow
418. *S. drummondiana* Barratt	Drummond willow
419. *S. exigua* Nutt.	narrowleaf willow
420. *S. geyeriana* Anderss.	Geyer willow
421. *S. lasiandra* Benth. var. *caudata* (Nutt.) Sudw.	whiplash willow

Santalaceae

422. *Comandra umbellata* (L.) Nutt.	bastard toadflax

Saxifragaceae

423. *Lithophragma tenella* Nutt.	slender woodland star

424. *P. palustris* L.	northern grass-of-Parnassus

SCROPHULARIACEAE

425. *Castilleja chromosa* A. Nels.	desert paintbrush
426. *C. linariifolia* Benth.	Wyoming paintbrush
427. *C. revealii* N. Holmgren	Bryce Canyon paintbrush
428. *Cordylanthus kingii* S. Wats.	King birdsbeak
429. *C. parviflorus* (Ferris) Wiggins	smallflower birdsbeak
430. *Mimulus guttatus* DC.	common monkeyflower
431. *M. rubellus* Gray	monkeyflower
432. *Orthocarpus luteus* Nutt.	yellow owlclover
433. *O. purpureo-albus* Gray	purple-white owlclover
434. *Pedicularis centranthera* Gray	dwarf lousewort
435. *Penstemon bracteatus* Keck	Platy penstemon
436. *P. caespitosus* Nutt. ex Gray	mat penstemon
437. *P. comarrhenus* Gray	dusty penstemon
438. *P. eatonii* Gray	firecracker penstemon
439. *P. leiophyllus* Pennell	Markagunt penstemon
440. *P. rostriflorus* Kellogg	beaked penstemon
441. *P. rydbergii* A. Nels.	Rydberg penstemon
442. *P. strictus* Benth.	Rocky Mountain penstemon
443. *P. utahensis* Eastw.	Utah penstemon
444. *Verbascum thapsus* L.	flannel mullein
445. *Veronica americana* Schw.	American brooklime

SINOPTERIDACEAE

446. *Cheilanthes feei* Moore	slender lipfern

SOLANACEAE

447. *Solanum triflorum* Nutt.	cutleaf nightshade

TAMARICACEAE

448. *Tamarix ramosissima* Ledeb.	salt cedar, tamarisk

VALERIANACEAE

449. *Valeriana acutiloba* Rydb.	cordilleran valerian
450. *V. edulis* Nutt.	taprooted valerian

VERBENACEAE

451. *Verbena bracteata* Lag. & Rodr.	prostrate vervain

VIOLACEAE

452. *Viola adunca* J. E. Smith	blue violet
453. *V. purpurea* Kellogg	pine violet

VISCACEAE

454. *Arceuthobium cyanocarpum* Coult. & Rose	limber pine dwarf mistletoe
455. *A. divaricatum* Engelm.	pinyon pine dwarf mistletoe
456. *A. douglasii* Engelm.	Douglas dwarf mistletoe
457. *A. vaginatum* (Willd.) Presl.	southwestern dwarf mistletoe
458. *Phoradendron juniperinum* Gray	juniper mistletoe

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INDEX TO GENERA AND COMMON NAMES

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DIFFERENTIAL RESPONSES TO NITROGEN FORM AND CONCENTRATION FOR *ORYZOPSIS HYMENOIDES* AND *ELYMUS LANCEOLATUS*

Robert S. Nowak[1], Cheryl L. Nowak[2], and Jay E. Anderson[3]

ABSTRACT.—In a greenhouse experiment, effects of nitrogen form and concentration on productivity and dry matter allocation differed between two species native to semiarid ecosystems of the Great Basin. Aboveground production of green surface area and of dry matter were consistently enhanced by increased nitrogen for the rhizomatous grass *Elymus lanceolatus* but not for the bunchgrass *Oryzopsis hymenoides*. These differences were likely due to inherently low growth rates of *O. hymenoides*. Aboveground dry matter allocation also differed between the two species. *O. hymenoides* had more leaves per tiller with increased nitrogen, whereas leaf size but not number increased for *E. lanceolatus*. Furthermore, increases in tiller density with increased nitrogen for *E. lanceolatus* were almost three times greater than those for *O. hymenoides*. *E. lanceolatus*, but not *O. hymenoides*, was sensitive to the form of nitrogen supplied to the plants. When NH_4–N was the only form of nitrogen supplied, high concentrations of NH_4–N inhibited aboveground production of *E. lanceolatus*.

Key words: dry matter production, dry matter allocation, ammonium-N, nitrate-N, nitrogen use efficiency, relative growth rate, Oryzopsis hymenoides, Elymus lanceolatus.

Water availability is generally acknowledged to be the abiotic factor that most limits productivity of semiarid vegetation (MacMahon and Schimpf 1981, Skujins 1981), and nitrogen is thought to be the second-most limiting factor (James and Jurinak 1978, Skujins 1981). However, evidence from field fertilization experiments that nitrogen limits productivity is not conclusive (Smith and Nowak 1990). Procedural problems may be partially responsible for the lack of a response to nitrogen fertilization in field trials. For example, low rates of application (James and Jurinak 1978, Fairbourn and Ranzi 1982) may not be sufficient to stimulate a statistically significant effect. Because the form of nitrogen affects plant growth (Bollard 1966, Smith et al. 1983), the form of nitrogen applied can also affect the vegetation responses. Of greater interest are biological and ecological processes that may influence the response of vegetation to fertilization. These processes include (1) loss of fertilizer nitrogen by volatilization or other processes (Klubek et al. 1978, Westerman and Tucker 1978), (2) inherently low growth rates of plants that are adapted to low nutrient environments (Chapin 1980), and (3) inherent differences among species in their responses to fertilization ([illegible] 1987).

Differentiating between procedural problems and ecological processes has made it difficult to clearly elucidate the relationships between plant productivity and the form or supply of nitrogen for plants in a natural, semiarid environment. However, experimentation in controlled environments minimizes problems associated with field experiments such as the following: (1) other growth conditions are optimized, (2) a range of application rates can be readily used, (3) different forms of nitrogen can be easily applied, and (4) individual responses of different species can be determined. Thus, we conducted a glasshouse experiment to determine the effects of nitrogen form and application rate on dry matter (DM) production and allocation for some representative Great Basin species.

Two forage grasses that are widely distributed throughout semiarid rangelands in the Great Basin and that represent two of the major growth forms of grasses were selected for this study: *Oryzopsis hymenoides* (R. & S.) Ricker and *Elymus lanceolatus* (Scribn. & J. G. Smith) Gould. Although the geographic distributions of these two species differ, they can occur together in native stands where their distributions overlap. *O. hymenoides* is a perennial bunchgrass that grows in cold-

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desert environments that receive less than 100 mm annual precipitation to over 200 mm (Robertson 1976, Jones 1990). Like *O. hymenoides*, *E. lanceolatus* is a native, perennial, drought-tolerant grass, but *E. lanceolatus* has a rhizomatous growth form. *E. lanceolatus* previously was known as *Agropyron dasystachyum* (Barkworth and Dewey 1985), and many authors also treat *E. lanceolatus* and *A. riparium* as synonyms (Hitchcock and Cronquist 1973, Cronquist et al. 1977, Barkworth and Dewey 1985). Because it was impractical to transplant *E. lanceolatus* plants into pots for our greenhouse experiment, a cultivar of *E. lanceolatus* called Sodar was used. Sodar is a naturally occurring variety that was released in 1954 as a special-purpose grass to provide groundcover rather than forage (Douglas and Ensign 1954). Sodar has been widely used for revegetation in the area from which we collected the *O. hymenoides* plants used for transplanting.

The primary objective of our study was to determine the effects of nitrogen form and application rate on DM production and allocation for these two semiarid species. Because DM production may also increase the surface area available for photosynthesis, we also measured green surface area. DM allocation was analyzed as changes in tiller production, number of leaves per tiller, leaf DM, sheath/stem DM, and root DM.

METHODS

Plant Establishment

Plants of *O. hymenoides* and *E. lanceolatus* were established in 12-L pots at plant densities that were representative of natural field conditions. Initial plant densities were 1 plant per pot for *O. hymenoides* and 15 per pot for *E. lanceolatus*. Pots were filled with clean sand, and 40 pots of each species were used. Plants of *O. hymenoides* were originally collected from the U.S. Department of Energy, Idaho National Engineering Laboratory, in late fall. The previous summer's growth had senesced by this time, and plants were dormant. One *O. hymenoides* plant was transplanted into each pot. Seeds of *E. lanceolatus* cv Sodar were germinated in petri dishes, and 15 seedlings were planted into each pot. All pots were placed in a greenhouse, where the experiments were conducted. Greenhouse air temperature varied from 20 °C at night to 30 °C during the day. Plants received only solar irradiance, which typically peaked at a photosynthetic photon flux density (PPFD) of 1.1 mmol m^{-2} s^{-1}.

After two months of growth, each species was sorted into four size classes based upon the number of tillers in the pot. Two replicates from each size class were randomly selected for a pretreatment destructive harvest (total sample size of eight pots per species). The remaining 32 replicates of each species were assigned to the eight nitrogen treatments with a stratified-random technique to insure adequate interspersion (Hurlbert 1984). At the initiation of the experiment, the pots with *O. hymenoides* had 62.1 ± 3.8 tillers per pot (average ± standard error) with 2.6 ± 0.1 green leaf blades (leaves) per tiller, whereas *E. lanceolatus* had 13.3 ± 0.3 tillers per pot with 5.2 ± 0.1 leaves per tiller.

Nutrient Solution Treatments

Ruakura nutrient solution (Smith et al. 1983) was selected for these experiments because pasture plants grown in Ruakura solution consistently yielded more DM than those grown in seven other nutrient culture solutions. The Ruakura solution has a 1:3 ratio of NH_4–N to NO_3–N, and concentrations of other nutrients do not appear to limit plant growth or to accumulate in toxic proportions. Eight experimental treatments were used that varied both the concentration and form of nitrogen (Table 1). Four concentrations of nitrogen with both forms of nitrogen in the nutrient solution were used: 25% (0.25), 50% (0.5), 100% (1.0), and 200% (2.0) of the full-strength concentration of nitrogen. In addition, two concentrations (0.25 and 2.0 of the full-strength nitrogen concentration) were used for solutions either with NH_4–N as the only nitrogen form or with NO_3–N as the only nitrogen form.

For our experiments, only the concentration of nitrogen in the nutrient solution was changed. The concentration of most other ions was held constant, as opposed to varying the concentration of all other ions in concert with nitrogen. To maintain the proper concentrations of the other nutrients, calcium, carbonate, and chloride salts were used as needed to prepare the nutrient solutions. Pots received 750-ml applications of the nitrogen solution [illegible] in the nutrient solutions used during the experiment.

[illegible] constant for all nutrient solutions.

Macronutrients

K = 238
S = 60
P = 40
Mg = 21
Na = 15

Micronutrients

Fe = 3.0
B = 0.5
Mn = 0.5
Zn = 0.25
Cu = 0.04
Mo = 0.01

Macronutrients whose concentration varied with different nutrient solutions:

Nutrient solution					
N[a]	Form of nitrogen	NO_3–N	NH_4–N	Ca	Cl
2.0	NH_4–N + NO_3–N	396	132	308	9
1.0	NH_4–N + NO_3–N	198	66	127	9
0.5	NH_4–N + NO_3–N	99	33	127	9
0.25	NH_4–N + NO_3–N	49.5	16.5	127	102
2.0	NO_3–N only	528	0	685	9
0.25	NO_3–N only	66	0	127	89
2.0	NH_4–N only	0	528	127	224
0.25	NH_4–N only	0	66	127	224

[a] Amount of total nitrogen in nutrient solution relative to full-strength Ruakura

twice weekly, and applications of nutrient solutions were alternated with tap watering.

Pretreatment Productivity Measurements

Dimensional measurements were used to estimate initial DM compartments of the treatment pots. Three tillers from each *E. lanceolatus* pot and five from each *O. hymenoides* pot were randomly selected for destructive harvest; more tillers were sampled from *O. hymenoides* because those pots had more tillers. The number of green leaves per tiller was counted, and the total length of all green leaves on a tiller and of all green sheaths and stems on a tiller was measured. For the eight pots of each species that were selected for the pretreatment harvest, projected areas and dry weights of leaves and of sheaths/stems on these same tillers were also measured.

Relationships between length and both area and weight were computed. Power regressions of length versus either area or weight had higher R^2 values than simple linear or log-linear regressions for *O. hymenoides*. A simple linear regression with an intercept of zero had the highest R^2 values for *E. lanceolatus*. The F-tests for all regression equations were significant; P was less than .001 for each regression. R^2 values averaged .88 for the eight regressions, with a range of .70–.98. These equations were then used to estimate the initial, pretreatment leaf area, leaf DM, sheath/stem area, and sheath/stem DM per tiller for the treatment pots. Total green area per tiller and total DM per tiller were calculated by summing the leaf and sheath/stem fractions. The initial leaf area index (LAI) of each treatment pot was estimated by multiplying the mean total area per tiller for that pot by the total number of tillers in that pot. Initial standing crop was the product of the mean total DM per tiller and the total number of tillers in that pot. Both LAI and standing crop were expressed on a pot area basis.

None of the pretreatment measurements of area or DM were significantly different among the experimental groups for both species (data not shown). Thus, replicate pots were adequately stratified among the experimental groups before the initiation of the treatments, and posttreatment differences among treatments can be attributed to effects of the nutrient solution rather than to initial differences in the experimental groups.

Posttreatment Productivity Measurements

Aboveground standing crop at the end of the experiment for each pot was determined with both destructive harvest and estimation techniques. We measured the number of green leaves per tiller as well as green leaf and green sheath/stem areas for three *E. lanceolatus* and five *O. hymenoides* randomly selected tillers. We also measured dry weights of both green and dead fractions for leaves and sheath/stems for these same tillers. Total green area per tiller and total (green plus dead) DM per tiller were calculated by summing the leaf and sheath/stem compartments. Posttreatment LAI and standing crop for each pot were estimated in the same manner as pretreatment values. Relative growth rates (RGR) of DM and of tillers were calculated from the pretreatment and posttreatment measurements of DM per tiller, standing crop, and number of tillers per pot. RGR was computed using the classical interval equation (Chiariello et al. 1989).

Three soil samples were taken from the center of each pot to determine belowground standing crop. Each sample was 237 ml (8 oz), and samples were taken from near the top of the soil surface, the middle of the soil profile, and near the bottom of the pot. The three samples were composited, and organic matter and soil particles were separated with a "root washer" (Smucker et al. 1982). Live roots were then separated from dead organic matter by a staining technique (Ward et al. 1978), dried, and weighed.

Plant and Soil Chemical Analyses

Total nitrogen concentrations for the green leaf, green sheath/stem, and senesced tissue compartments were determined with a CHN analyzer (Perkin-Elmer Model 2400). All green leaves on the three *E. lanceolatus* tillers that were harvested in each pot were pooled together, then ground to 40-mesh size. Similarly, all green sheath/stem and senesced tissue fractions from *E. lanceolatus* tillers as well as green leaf, green sheath/stem, and senesced fractions for the five *O. hymenoides* tillers were pooled and ground. The nitrogen concentration of each fraction was multiplied by the respective dry weight, and those products were then summed to calculate a total weight of nitrogen, or nitrogen pool size, per tiller. Tiller nitrogen pool size was multiplied by the total number of tillers in that pot to determine nitrogen standing crop for each pot. Finally, the amount of aboveground DM produced per unit of aboveground nitrogen uptake, which we term nitrogen use efficiency (NUE), was calculated from the ratio of posttreatment standing crop minus initial standing crop to posttreatment nitrogen standing crop minus initial nitrogen standing crop.

To determine soil properties, we took a second set of soil samples adjacent to the root samples. Soil analyses were conducted by the Soil Analysis Laboratory of the Nevada Agricultural Experiment Station using standard techniques. Electrical conductivity (EC) and pH of the soil water were determined following the methods of Richards (1954). Ca, Mg, and Na were determined on saturation extracts with an atomic absorption spectrometer (Perkin-Elmer Model 5000). Total nitrogen in the soil was determined with Kjeldahl analysis modified to include NO_3–N. These same soil chemical properties were also determined for soil samples taken from the pretreatment, destructive harvest pots.

Statistical Analyses

Analysis of variance (AOV) techniques were used for data analyses. One-way AOVs were used to determine if pretreatment DM measurements differed among the eight experimental groups. Posttreatment soil chemical properties and plant productivity were analyzed with a two-step procedure because our experimental design had missing cells; i.e., the two intermediate nitrogen concentrations were not used for the solutions with NH_4–N only or with NO_3–N only. The first statistical analysis was to determine the interactive effects of nitrogen form and concentration on DM production and allocation. Each species was analyzed with separate two-way AOVs. Each AOV had two main effects: nitrogen form in the nutrient solutions (three levels: NO_3–N only, NH_4–N only, and both forms) and nitrogen concentration in the nutrient solutions (two levels: 0.25 and 2.0). For significant terms in the AOVs, means were compared with LSD techniques, taking into account the appropriate precautions (Snedecor and Cochran 1967). The second statistical analysis had two objectives: first, to determine if DM production and allocation changed linearly with the concentration of nitrogen in the nutrient solution; and second, to determine if this relationship differed between the two species. Split-plot AOVs with covariance analysis and linear contrasts were used in this second step. Nitrogen concentration in the nutrient solutions (four levels: 0.25, 0.5, 1.0, and 2.0) was the main plot treatment factor, with species (two levels) as a split-plot factor. Because of the initial differences between species, pretreatment area and DM measurements were used as covariates for each respective posttreatment variable. Coefficients for the linear contrasts were calculated according to procedures described in Gomez and Gomez (1984). For all statistical analyses, $P < .05$ was considered significant.

RESULTS

Effects of Solution Nitrogen Form on Productivity

DM PRODUCTION AND ALLOCATION.—The form of nitrogen influenced aboveground productivity and allocation of *E. lanceolatus* but did not significantly affect root DM nor root:shoot ratios (Table 2). The effects of nitrogen form on DM production and allocation occurred primarily at the high concentration of nitrogen. Although the nitrogen form main effect was significant for only the four measurements of green surface area, all but four of the dependent variables had a significant interaction term. For each of the dependent variables that had a significant interaction term in the 2-way AOV, DM production for pots supplied either with both forms of nitrogen or with NO_3–N only increased with increased nitrogen concentration. However, the corresponding measurement of DM production for pots supplied with the 0.25 NH_4–N only nitrogen solution was not significantly greater than that for pots supplied with the 2.0 NH_4–N only nitrogen solution. Thus, close inspection of the interaction terms showed that inhibitory effects of nitrogen form occurred only if a high concentration of NH_4–N was the sole source of nitrogen.

The form of nitrogen did not affect DM production or allocation of *O. hymenoides* (data not shown). Neither the interaction term nor the nitrogen form main effect was significant in the 2-way AOVs for the same 15 variables listed for *E. lanceolatus* in Table 2.

TISSUE NITROGEN CONTENT AND NITROGEN USE EFFICIENCY.—For *O. hymenoides*, the effects of the form of nitrogen varied among the different nitrogen compartments (Table 3). The main effect of nitrogen form was not significant for the concentration of nitrogen in green sheath/stem tissue, the total pool size of nitrogen in a tiller, and the total aboveground pool size of nitrogen in a pot. For senesced tissue, mean nitrogen concentration of tissue from pots that received both forms of nitrogen was significantly lower than that for plants that received only one form of nitrogen. For green leaf tissue, tissue nitrogen concentration for plants that received either both forms of nitrogen or NO_3–N only was significantly lower than that for plants that received NH_4–N only. However, NUE of plants that received NH_4–N only was significantly lower than NUE of those that received either both forms of nitrogen or NO_3–N only.

For *E. lanceolatus*, the form × concentration interaction terms were significant for four of the six nitrogen compartments: leaf nitrogen concentration, tiller nitrogen content, nitrogen standing crop, and NUE (Table 3). For these four compartments, means for different forms of nitrogen in the 0.25 nutrient solutions were not significantly different. For the 2.0 nutrient solutions, means for leaf nitrogen concentration, tiller nitrogen content, and nitrogen standing crop with both forms of nitrogen were significantly greater than means for those compartments either with NH_4–N only or with NO_3–N only. Mean NUE with both forms of nitrogen was, however, significantly less than that with NH_4–N only or NO_3–N only. The main effect of nitrogen form was significant for nitrogen concentration of senesced tissue: mean concentration for pots that received NH_4–N only was significantly greater than for pots that received NO_3–N only, but the mean for pots that received both forms of nitrogen solution was not significantly different from the other two means.

Effects of Solution Nitrogen Concentration on Productivity

DM PRODUCTIVITY AND ALLOCATION.—The effects of increased nitrogen concentration on green surface area and DM production were significantly greater for *E. lanceolatus* than for *O. hymenoides* (Fig. 1). Over the range of nitrogen concentrations used, both green area and DM of *E. lanceolatus* increased linearly with nitrogen concentration for measurements on a leaf, tiller, and ground area basis (Figs.

TABLE 2. AOV, means, and mean comparisons for effects of nitrogen form at two levels of nitrogen concentration on DM compartments of *E. lanceolatus*.

	AOV table[a]			Means[b]					
	Main effects			0.25 N solution			2.0 N solution		
DM compartment	N form	N conc	Interaction	A+N	A only	N only	A+N	A only	N only
Green sheath/stem area (cm² tiller⁻¹)	0.042	0.001	0.008	0.44*a*	0.54*a*	0.54*a*	1.11*b*	0.49*a*	0.90*b*
Green leaf area (cm² tiller⁻¹)	0.001	0.012	0.001	10*a*	11*ab*	15*bc*	20*d*	8*a*	17*cd*
Total green surface area (cm² tiller⁻¹)	0.001	0.010	0.001	10*a*	12*ab*	15*bc*	21*d*	9*a*	18*cd*
Leaf area index	0.002	<0.001	<0.001	7*a*	11*ab*	13*b*	26*d*	9*ab*	20*c*
Green sheath stem DM (mg tiller⁻¹)	NS	NS	NS	10	60	16	30	13	20
Green leaf DM (mg tiller⁻¹)	NS	0.040	0.004	55*a*	73.3*ab*	80*ab*	111*c*	57*a*	90*bc*
Total (green + dead) DM (mg tiller⁻¹)	NS	NS	0.006	90*a*	162*b*	131*ab*	179*b*	88*a*	151*ab*
Standing crop (kg m⁻²)	NS	0.005	<0.001	0.6*a*	1.4*bc*	1.1*abc*	2.3*d*	0.9*ab*	1.6*cd*
Root DM (g l)	NS	NS	NS	4.8	4.2	1.2	3.1	1.1	5.0
Root:shoot ratio	NS	0.003	NS	1.83	0.82	0.95	0.30	0.31	0.71
Number of green leaves per tiller	NS	NS	NS	4.4	4.6	4.6	4.4	4.6	4.5
Tiller density (number cm⁻²)	NS	<0.001	0.035	0.66*a*	0.89*ab*	0.81*ab*	1.30*c*	1.02*b*	1.11*bc*
Tiller DM RGR (mg g⁻¹ day⁻¹)	NS	NS	0.001	20*ab*	26*bc*	21*abc*	30*c*	19*a*	25*bc*
Crop DM RGR (mg g⁻¹ day⁻¹)	NS	0.001	<0.001	61*a*	71*c*	69*bc*	80*d*	66*ab*	72*c*
Tiller number RGR (% day⁻¹)	NS	<0.001	0.001	1.1*a*	1.5*b*	1.5*b*	5.0*d*	1.7*bc*	1.8*cd*

[a] *P* values for the [illegible] AOV. NS indicates the term was not significant, *P* > .05.
[b] Means [illegible] that received both [illegible] (A+N), that received NH_4-N only (A only), and that received NO_3-N only (N only). Means within a row with the same letter were not significantly different.

TABLE [illegible]. AOV [illegible] and mean comparisons for effects of nitrogen form at two levels of nitrogen concentration on nitrogen content of DM compartments and nitr[illegible] [illegible] and *E. lanceolatus*.

[illegible]	AOV table[a]			Means[b]					
	Main effects			0.25 N solution			2.0 N solution		
	N form	N conc	Interaction	A+N	A only	N only	A+N	A only	N only
[illegible]									
Senesced tissue N concentration (%)	0.017	0.035	NS	1.1	1.5	1.5	1.4	1.9	1.7
Sheath/stem N concentration (%)	NS	NS	NS	2.1	2.2	2.6	2.6	2.6	2.1
Leaf N concentration (%)	0.001	<0.001	NS	3.8	4.5	3.8	4.7	5.5	4.5
Tiller N content (mg tiller^{-1})	NS	0.027	NS	2.4	2.5	1.9	2.6	3.4	2.9
N standing crop (g m^{-2})	NS	0.001	NS	9	12	11	15	20	18
Nitrogen use efficiency (g DM g^{-1} N)	0.001	<0.001	NS	46	32	42	31	25	30
E. lanceolatus									
Senesced tissue N concentration (%)	0.029	<0.001	NS	1.0	1.1	1.0	2.1	2.3	1.7
Sheath/stem N concentration (%)	NS	<0.001	NS	1.7	1.7	1.7	2.4	2.1	2.5
Leaf N concentration (%)	<0.001	<0.001	<0.001	3.1*ab*	2.8*a*	3.1*ab*	4.7*c*	3.1*ab*	3.2*b*
Tiller N content (mg tiller^{-1})	0.020	0.002	<0.001	2.1*a*	3.5*ab*	3.1*ab*	6.8*c*	2.4*a*	4.0*ab*
N standing crop (g m^{-2})	0.002	<0.001	<0.001	14*a*	30*ab*	26*a*	86*c*	24*a*	44*b*
Nitrogen use efficiency (g DM g^{-1} N)	0.001	<0.001	0.010	43*c*	47*c*	43*c*	26*a*	37*b*	37*b*

[a] P values for the two main effects and the interaction term from 2-way AOVs. NS indicates that the term was not significant ($P > .05$).

[b] Means for pots that received both forms of nitrogen (A+N), that received NH_4–N only (A only), and that received NO_3–N only (N only). Means within a row with the same letter were not significantly different.

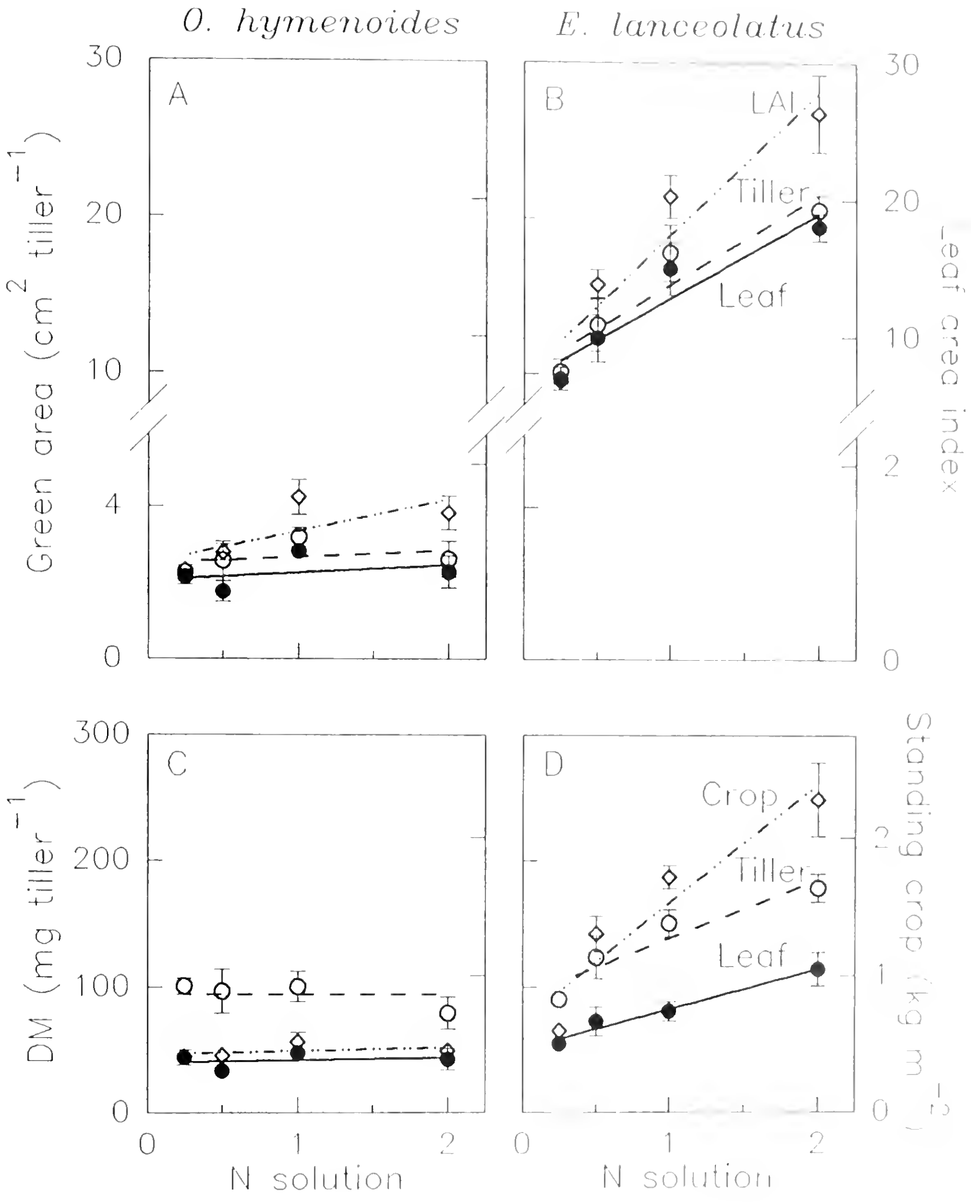

Fig. 1. Aboveground green surface area and DM for *O. hymenoides* (A, C) and *E. lanceolatus* (B, D) at the end of the greenhouse experiment. Means and standard error bars at each concentration of nitrogen in the nutrient solution are given. A, B: Green leaf area per tiller (solid circles, solid lines), total green area per tiller (open circles, dashed lines), and green leaf area index (diamonds, dash-dot-dot lines). C, D: Leaf DM per tiller (solid circles, solid lines), total DM per tiller (open circles, dashed lines), and aboveground standing crop (diamonds, dash-dot-dot lines). Lines are linear regressions of the data if linear contrasts were significant or horizontal lines if the linear contrasts were not significant.

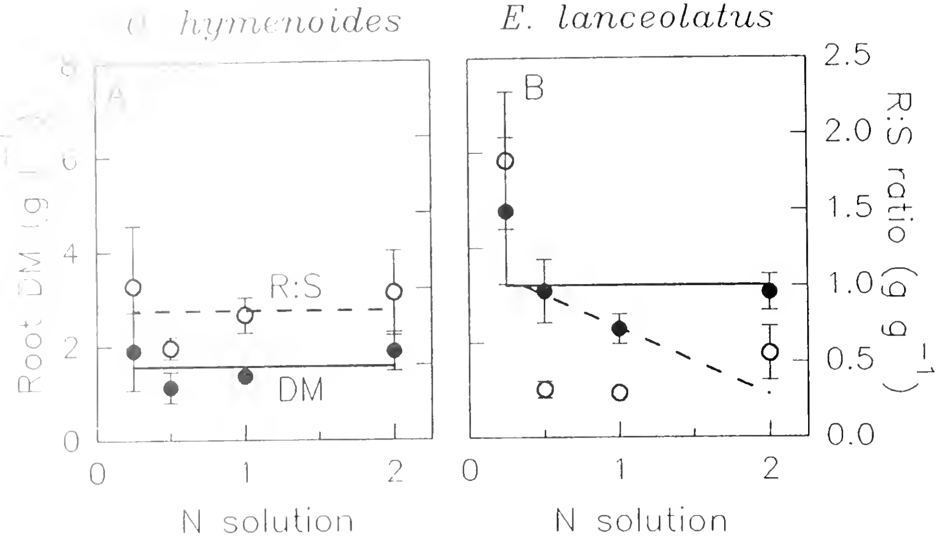

Fig. 2. Belowground DM for *O. hymenoides* (A) and *E. lanceolatus* (B) at the end of the experiment. A, B: Root DM (solid circles, solid lines) and root:shoot ratio (open circles, dashed lines). Other graph characteristics are as given in Figure 1.

1B, 1D). Although the linear contrasts of the three area measurements with nitrogen concentration were significant for *O. hymenoides* (Fig. 1A), these increases in surface area with nitrogen concentration were much less than those for *E. lanceolatus* (Fig. 1B). For the DM compartments of *O. hymenoides* (Fig. 1C), linear contrasts were significant for leaf and standing crop DM, but not for tiller DM.

Root DM was not affected by nitrogen concentration in either species (Figs. 2A, 2B). Root DM for *E. lanceolatus*, however, was significantly greater than that for *O. hymenoides* at all nitrogen concentrations. Root:shoot (R:S) ratios of *E. lanceolatus* significantly decreased with increased nitrogen concentration, whereas those of *O. hymenoides* were unaffected by nitrogen concentration. Although R:S ratios were not significantly different between species at low nitrogen concentrations, they were significantly greater for *O. hymenoides* at high nitrogen concentrations.

Tiller density increased with increased nitrogen concentration for both species (Fig. 3). Tillers of *O. hymenoides* grown at high nitrogen concentrations also had more green leaves per tiller than those grown at low nitrogen concentrations (Fig. 3A). However, the number of leaves per tiller for *E. lanceolatus* was unaffected by nitrogen concentration (Fig. 3B). Finally, both tiller density and number of green leaves per tiller for *E. lanceolatus* were significantly greater than those for *O. hymenoides*.

Except for DM per tiller for *O. hymenoides* (Fig. 4A), increased nitrogen concentration increased RGR (Fig. 4). In addition, RGR of DM on a tiller basis, of DM on a crop basis, and of tiller number for *E. lanceolatus* (Fig. 4B) were significantly greater than those for *O. hymenoides* (Fig. 4A).

TISSUE NITROGEN CONTENT AND NITROGEN USE EFFICIENCY.—The concentration of nitrogen had a significant effect on tissue nitrogen concentration of both species (Figs. 5A, 5B). Tissue nitrogen concentrations increased with increased concentration of nitrogen. Nitrogen concentrations of green tissues were significantly greater for *O. hymenoides* than for *E. lanceolatus* except at the highest solution nitrogen concentration. For senesced tissue, tissue nitrogen concentrations were similar for both species at low solution nitrogen concentrations, but *E. lanceolatus* had significantly higher tissue nitrogen concentrations than *O. hymenoides* at the high solution nitrogen concentration.

Aboveground pool sizes of tissue nitrogen significantly increased with solution nitrogen

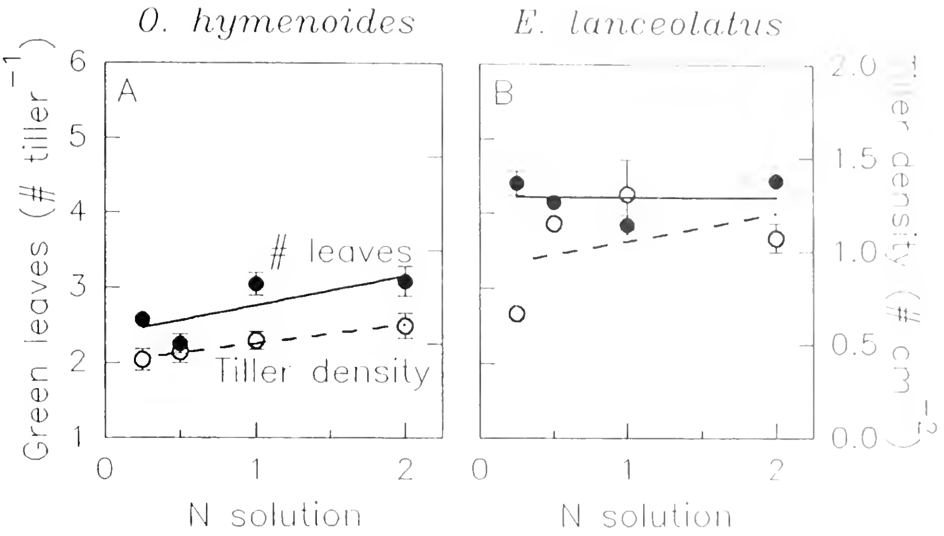

Fig. 3. Number of green leaves per tiller (solid circles, solid lines) and tiller density (open circles, dashed lines) for *O. hymenoides* (A) and *E. lanceolatus* (B) at the end of the experiment. Other graph characteristics are as given in Figure 1.

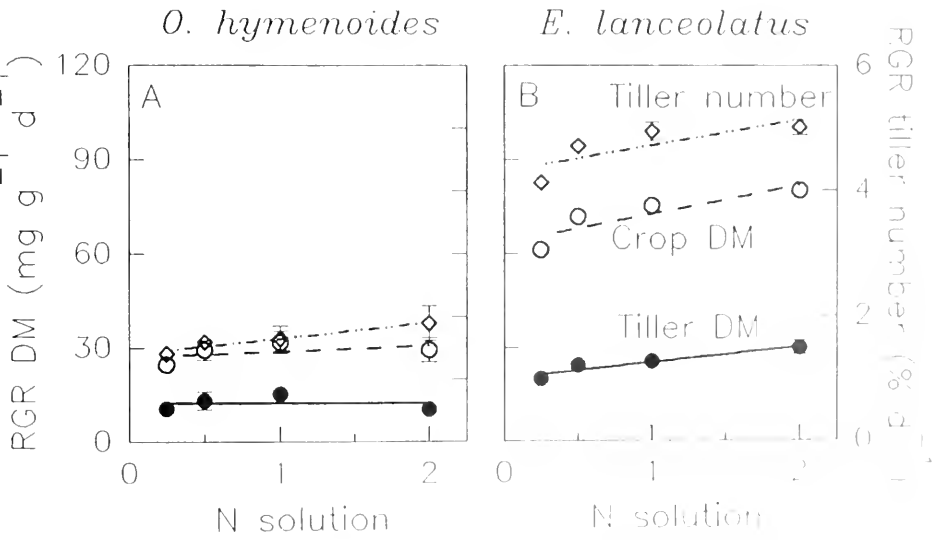

Fig. 4. Relative growth rates for *O. hymenoides* (A) and *E. lanceolatus* (B) over the duration of the experiment. Mean RGRs at each level of nitrogen concentration in the nutrient solution are given for DM production per tiller (solid circles, solid lines), total aboveground DM production (open circles, dashed lines), and number of tillers (diamonds, dash-dot-dot lines). Other characteristics of the graph are as given in Figure 1.

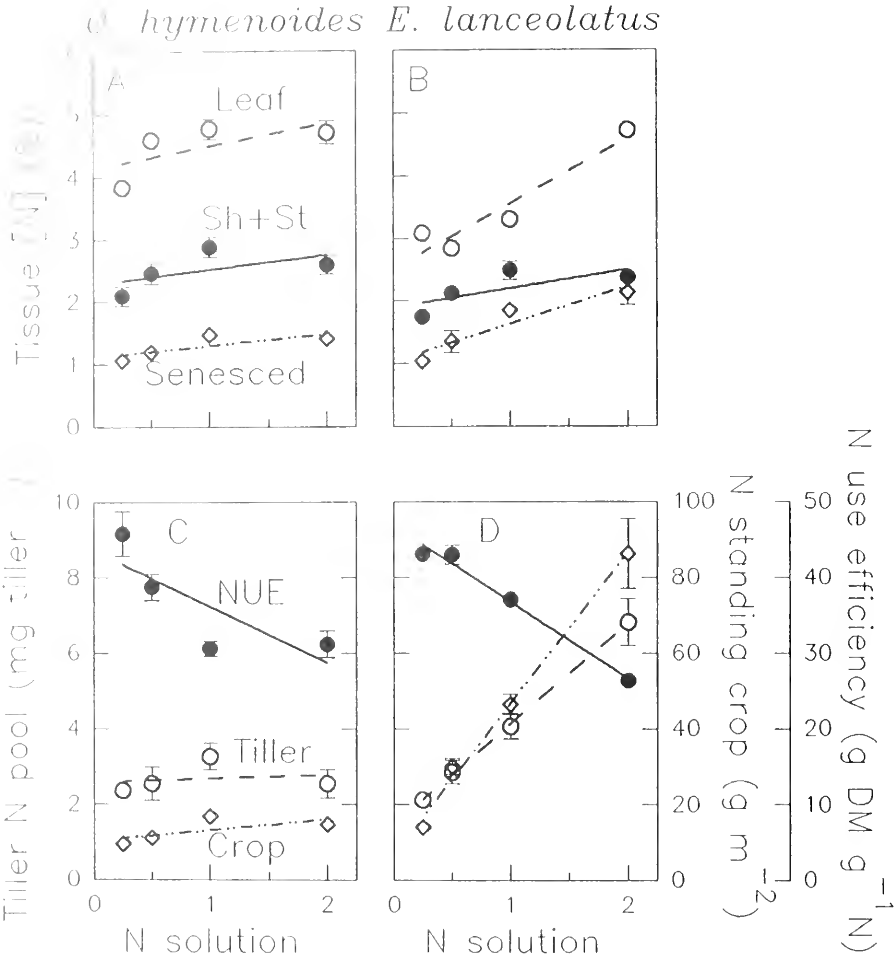

Fig. 5. Nitrogen concentrations, pool sizes, and use efficiencies for aboveground DM for *O. hymenoides* (A, C) and *E. lanceolatus* (B, D). A, B: Nitrogen concentrations of leaves (open circles, dashed lines), sheaths/stems (solid circles, solid lines), and senesced tissues (diamonds, dash-dot-dot lines). C, D: Total pool size of nitrogen in tillers (open circles, dashed lines), total pool size of nitrogen in the aboveground standing crop (diamonds, dash-dot-dot lines), and nitrogen use efficiency (solid circles, solid lines). Other graph characteristics are as given in Figure 1.

concentration for both species, but NUE decreased with increased solution nitrogen concentration (Figs. 5C, 5D). Nitrogen pool size (expressed either as the total amount of nitrogen per tiller or as the total amount of nitrogen in the crop) were not significantly different between species at low solution nitrogen concentrations, but nitrogen pool sizes at higher solution nitrogen concentrations for *E. lanceolatus* were significantly greater than those for *O. hymenoides*. NUE, i.e., the amount of aboveground DM produced per amount of nitrogen taken up, was not significantly different between species.

Soil Chemical Properties

The form and concentration of nitrogen in the nutrient solution had only minor effects on soil chemical properties. Of particular interest was soil pH. Nitrogen form significantly affected the pH of soils from *O. hymenoides* pots: pH of soils that received both forms of nitrogen (7.6) was slightly but significantly lower than pH of soils that received either NH_4–N only (7.8) or NO_3–N only (7.9). Small but significant differences in pH among nitrogen-concentration groups also occurred, but only for soils from *E. lanceola-*

TABLE 4. Pretreatment (Pretrt) and posttreatment chemical properties of soil samples composited from each pot and analyzed by standard soil techniques.

		Nitrogen solution[a]			
Edaphic property	Pretrt	0.25	0.5	1.0	2.0
O. hymenoides					
pH	7.6	7.8	7.7	7.8	7.7
Cations					
Ca (meq l^{-1})	1.0	9.5*a*	6.2*a*	20.4*a*	39.9*b*
Mg (meq l^{-1})	0.8	2.4*a*	1.6*a*	4.5*b*	1.9*b*
Na (meq l^{-1})	1.6	2.8	2.3	3.6	2.6
EC (dS m^{-1})	0.4	1.2*a*	0.9*a*	2.2*a*	5.1*b*
Nitrogen					
Total N (µg g^{-1})	71	158*a*	273*a*	689*a*	1535*b*
E. lanceolatus					
pH	8.2	8.0*b*	8.3*c*	8.5*c*	7.8*a*
Cations					
Ca (meq l^{-1})	3.4	7.3*a*	5.3*a*	11.7*a*	21.3*b*
Mg (meq l^{-1})	0.7	1.7	1.1	2.1	2.9
Na (meq l^{-1})	1.5	2.9*a*	1.2*b*	3.0*ab*	2.3*a*
EC (dS m^{-1})	0.5	1.0*a*	1.2*a*	1.4*ab*	2.2*b*
Nitrogen					
Total N (µg g^{-1})	82	69*a*	78*a*	108*b*	773*c*

[a] Statistical differences among posttreatment means are indicated by different letters in a row; rows without letters indicate that the AOV terms were not significant.

tus pots (Table 4). For both species, Ca concentration was significantly greater only at the highest nitrogen concentration (Table 4), but nitrogen form did not affect Ca concentration (data not shown). Except for total soil nitrogen, the effects of form (data not shown) and concentration (Table 4) of solution nitrogen were either not significant or significant but of small magnitude. Total soil nitrogen significantly increased with increased concentration of nitrogen in the nutrient solution for both species (Table 4).

DISCUSSION

Effect of Solution Nitrogen Form on Productivity

Aboveground DM production and allocation for *E. lanceolatus* were sensitive to the form of nitrogen in the nutrient solution, whereas those for *O. hymenoides* were not. This sensitivity of *E. lanceolatus* to nitrogen form does not appear to be induced by soil pH. Productivity can be inhibited by acidification of the substrate in the presence of NH_4–N (Thomas et al. 1987) accompanied by a low pH-induced inhibition of NH_4–N uptake (Vessey et al. 1990), but pH of soils from *E. lanceolatus* pots was slightly alkaline and not significantly affected by the form of nitrogen in the solution. More likely, this sensitivity to nitrogen form in *E. lanceolatus* is due to some species-specific characteristics of nutrient uptake or assimilation. For example, *E. lanceolatus* may have a low level of glutamine synthetase activity, which detoxifies NH_4–N in plants (Magalhaes and Huber 1989). The fact that inhibition occurred at high concentrations of NH_4–N but not at low concentrations is consistent with this mechanism. A low level of glutamine synthetase activity would allow uptake and assimilation of low NH_4–N concentrations from the 0.25 nutrient solution, but the high NH_4–N concentrations immediately following treatment with the 2.0 nutrient solution may have exceeded the plant's enzymatic capacity and thus had toxic effects on the plants.

Effects of Solution Nitrogen Concentration on Productivity

Aboveground DM production of *E. lanceolatus* was consistently enhanced by increased nitrogen availability, whereas that of *O. hymenoides* was not. The difference between

O. hymenoides and *E. lanceolatus* cannot be attributed simply to differences in their native habitats, to differences in growth form, to differences in storage of nitrogen within tissues, or to low supplies of soil nitrogen. Plants from less fertile sites are often less responsive to nutrient supply than those from more fertile environments (Chapin 1980). Although *O. hymenoides* is generally found on slightly coarser soils than *E. lanceolatus*, both species intermingle in the area from which we collected the *O. hymenoides* plants. It is also very unlikely that the cultivar of *E. lanceolatus* used in our greenhouse experiment was inadvertently selected for response to applied nitrogen for three reasons. First, the original accession for Sodar was a naturally occurring variety, and field trials were conducted on native, unfertilized soils. Second, the cultivar was released for its ability to form a groundcover under dry conditions rather than for its forage production (Douglas and Ensign 1954). Third, our field experiments with native plants of both species show similar results (Smith and Nowak 1990, Nowak et al. manuscript). Thus, these two species share similar habitats but differ in their response to nitrogen supply. The differences in nitrogen response between the rhizomatous grass *E. lanceolatus* and the bunchgrass *O. hymenoides* also cannot be attributed to a difference in growth form. For example, other Great Basin bunchgrasses such as *Agropyron cristatum* (Holechek 1982), *A. desertorum* (Sneva 1973), and *Stipa thurberiana* (Miller et al. 1991) have increased DM production with nitrogen fertilization. Thus, at least some grasses of each growth form in the Great Basin respond to nitrogen fertilization. Luxury consumption, i.e., resource acquisition in excess of resource use for current growth, is a mechanism in plants from nutrient-poor environments to acquire and store nutrients for future growth (Bloom et al. 1985). In our study, tissue nitrogen concentrations of both species increased with increased level of nitrogen in the nutrient solution. Thus, the increased nitrogen concentration in tissues appears to be a generalized response of both grass species to increased nitrogen availability rather than a mechanism to acquire and store nitrogen for future growth. Finally, low rates of nitrogen application [illegible] loss of fertilizer nitrogen may preclude a [illegible] response in field experiments. Because soil nitrogen content of *O. hymenoides* pots was at least twice that of pretreatment nitrogen contents and because soil nitrogen increased with increased solution nitrogen concentrations, soil nitrogen supply did not limit *O. hymenoides* growth.

The most parsimonious explanation for this difference between species in their response to nitrogen supply is that *O. hymenoides* has inherently low growth rates. Even under the nearly ideal growth conditions in our greenhouse experiment, low levels of solution nitrogen were adequate for *O. hymenoides* growth. The relatively high nitrogen content of *O. hymenoides* leaves (4–5%) also indicates that nitrogen supply was adequate. The low growth rates of *O. hymenoides* are partially due to meristematic limitations. For example, the proportional increase in tiller density from the 0.25 to the 2.0 level of nitrogen was almost three times greater for *E. lanceolatus* than for *O. hymenoides*. Intercalary meristems of *O. hymenoides* were also limited: the size of individual leaves was not significantly affected by the nitrogen solution, whereas that for *E. lanceolatus* progressively increased with the nitrogen content of the nutrient solution.

DM allocation also differed between species. Root:shoot ratios of *E. lanceolatus* plants decreased with increased nitrogen content of the nutrient solution, but nitrogen concentration did not affect belowground DM production of either species. Thus, the decreased root:shoot ratios for *E. lanceolatus* are primarily due to the increase in aboveground DM with increased nitrogen concentration. However, the lack of an effect of nitrogen availability on root production may be an artifact of the limited rooting volume in the pots. For example, results from field experiments with *E. lanceolatus* differed from our greenhouse experiment: root production and root:shoot ratios increased with fertilization in the field (Holechek 1982).

Changes in DM production and allocation can be primarily attributed to nitrogen concentration in the nutrient solutions rather than to other soil chemical properties. Although EC and cation concentrations of the soils increased with the nitrogen content of the nutrient solutions, EC values were within the range that does not show any adverse effect for many forage species (Western Fertilizer Handbook 1985). Furthermore, both *O.*

hymenoides and *E. lanceolatus* tolerate low to moderate salinity (Douglas and Ensign 1954, Robertson 1976). Because the concentrations of most other ions were kept constant in the nutrient solutions, variation in the concentrations of other nutrients also did not confound the experiment.

In summary, these two co-existing, perennial grasses from semiarid habitats in the Great Basin respond differently to both form and amount of plant-available nitrogen under ideal growth conditions. Physiological responses to nitrogen fertilization in field experiments also differed among species from the same vegetation type (Toft et al. 1989). These results indicate that the variation in responses to nitrogen fertilization in field trials may be partially due to species-specific characteristics. Thus, procedural problems alone do not account for the lack of response to nitrogen fertilization in field trials. The extent to which these differential, species-specific responses to nitrogen influence community dynamics is unknown, but warrants further study.

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SEEDLING SIZE AND SURVIVAL FOR *CHRYSOTHAMNUS NAUSEOSUS*

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ABSTRACT.—Seedling size and survival in relation to summer drought were examined for *Chrysothamnus nauseosus* growing under field and greenhouse conditions. In the field, summer survival rates were less than 2% annually for the three years monitored. The effect of initial seedling height on subsequent survival was examined in both the field and greenhouse by grouping seedlings into live and dead categories on each census date and comparing the initial heights for seedlings in these categories. For a majority of the census dates, the initial height of surviving seedlings was greater than the initial height of those that subsequently died (significant differences ranged from 4 to 8 mm), indicating that seedlings that were taller at the initiation of the drought period had a higher probability of survival. In the greenhouse, taller seedlings had greater shoot and root biomass and rooting depth. Seedlings that are larger (i.e., taller and have greater aboveground biomass) in late spring appear to have a higher probability of surviving the summer drought due to greater rooting depth and hence increased access to moisture in deeper soil layers. Seed availability and safe sites for germination were probably not limiting since large numbers of seedlings successfully germinated in a patchy pattern during the study period. Seedling size and probability of survival were not related to either seedling density or the distance to nearest seedling neighbor. Survival through summer drought appears to be the main limitation to seedling recruitment in this population.

Key words: seedlings, survival, size, distribution, rabbitbrush, Chrysothamnus.

Seedling recruitment is crucial for the maintenance of most plant populations. However, high mortality rates are often associated with the seedling life history stage, and the patterns of reproductively mature individuals in a community may reflect primarily the historical effects of mortality during the seedling stage. Many seedling deaths are attributed to water stress though other abiotic and biotic factors are often involved (Harper 1977, Cook 1979, Fenner 1985). The small size of a newly germinated seedling places it near the soil surface where the largest fluctuations in soil temperature and soil moisture occur (Drew 1979, Caldwell 1985). When soil moisture is lost from shallow layers through evaporation and transpiration, a small root system has limited access to water in deeper soil layers, and the seedling is susceptible to water stress (Harper 1977, Angevine and Chabot 1979, Cook 1979). Even though germination and seedling growth may be timed to minimize the impact of the drought (Beatley 1974, Went 1979), new recruits of perennial species in semiarid environments must be able to persist through a drought during their first year.

The climate of the Great Basin is characterized by cold (below freezing) winters and warm summers where temperatures often exceed 40° C. Soil moisture recharge occurs in late winter and early spring when evaporation is low, and then the lowest monthly precipitation rates co-occur with the high summer temperatures. Summer precipitation events are usually of high intensity and short duration, so that moisture generally does not penetrate deep into the soil. Hence, the Great Basin generally has a hot, dry period from June through August when soil moisture is progressively depleted from surface soil layers (Campbell and Harris 1977, Caldwell 1985). The patterns of precipitation and soil moisture recharge, combined with the tendency to have fine soils, lead to the predominance of grassland and shrub communities in the lower elevations of the Great Basin (West 1988).

Chrysothamnus nauseosus (Pallas) Britt., commonly called rubber rabbitbrush, is a winter-deciduous shrub common throughout the Great Basin. Reproductively mature individuals are deep rooted in comparison to other woody plants in the communities and depend mainly on soil moisture recharged by winter and spring precipitation (Branson et al. 1976, Klepper et al. 1985, Flanagan and Ehleringer 1991, Flanagan et al. 1992, Donovan and Ehleringer in press). Seeds generally germinate in the spring after snowmelt, and both

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seedlings and juveniles of *C. nauseosus* are more water stressed than larger, reproductively mature individuals during drier parts of the growing season (Donovan and Ehleringer 1991, 1992, in press). The pattern of small plants being more water stressed is presumably a function of having shallow roots and is consistent with recent studies in other water-limited habitats (DeLucia and Schlessinger 1990, Knapp and Fahnestock 1990, Cui and Smith 1991). If seedlings are dying as a result of water stress because they have shallow roots, then larger seedlings with deeper roots at the beginning of a drought should have an increased probability of drought survival (Cook 1980).

The objectives of the study were to investigate characteristics related to *C. nauseosus* seedling survival: (1) the timing and extent of seedling mortality in a natural population, (2) the effect of seedling size on subsequent survival during a drought, and (3) the effect of seedling density and distance to mature individuals on both germination and survival.

METHODS

Field Site and Field Studies

The Range Experiment Field Station at Tintic, Utah (39°55' N, 122°03' W, elevation 1775 m), was the site for the field studies as well as the source site for seeds used in the greenhouse studies. *Artemisia tridentata* Nutt. and *Juniperus osteosperma* (Torr.) Little dominated the site until it was cleared and disc-plowed in the early 1950s. Since then the site has recovered, with cattle grazing limited to approximately two weeks each spring except for the study years, during which cattle were excluded. The site, currently occupied by *A. tridentata*, *C. nauseosus* ssp. *hololeucus*, and perennial bunchgrasses, is most closely associated with the higher elevations of the Sagebrush Steppe vegetation type (West 1988). Soils are sandy loams (Jensen 1983), and the area receives an average of 374 mm of precipitation annually (Owens 1987). Monthly precipitation amounts for the study period were recorded by weather monitoring stations maintained at the Tintic Station by Utah State University personnel. Soil moisture values were determined gravimetrically. Percent soil moisture was converted to soil water potential using a [illegible] soil moisture retention curve developed using soil psychrometers (Wescor PR-55).

Seedling plots were located in a naturally established population of *C. nauseosus*. For 1989–91 seedlings were monitored in square plots 0.3 m to a side and located within 0.5 m of large, reproductively mature shrubs; four plots were established in 1989, and two more were added in 1990. Forty additional seedling plots (designated 1991–40) were established in 1991, each 0.28 × 0.43 m. Within plots, seedling locations were marked with toothpicks, and plots were censused at intervals throughout the growing seasons for number of surviving seedlings. Yearly comparisons of seedling density include only the four plots established in 1989 and monitored consistently throughout the three years.

Of the 1991–40 plots, 20 were randomly located throughout the population, except for avoiding the stems of large shrubs and/or clumps of perennial grasses. The distance was measured from the seedling plots to nearest large shrub of *C. nauseosus* or other woody shrub. The remaining 20 plots were arranged around five mature *C. nauseosus* shrubs, one at each of the four compass directions and 0.5 m distance from the base of the shrub. The 1991–40 plots were characterized visually for percent groundcover of small herbs and annual grasses. Seedlings in each of these plots were initially mapped on a grid, and individual seedlings measured for height (to top of longest leaf) at each census date. Plants were declared dead when they appeared to lack chlorophyll and were brittle.

Greenhouse Studies

Two studies were conducted with *C. nauseosus* plants growing in pots, using the Tintic population as the seed source. For the first study, designated GS1, plants were grown outside the greenhouse during the summer, concurrently with the monitoring of seedlings at the Tintic site during the 1991 season. Seedlings were grown in 1-m-tall pots of 15-cm-diameter PVC (polyvinyl chloride) pipe with bottom caps and drainage holes. The soil mixture consisted of one-third sand, one-third perlite, and one-third mixture of topsoil, organic material, and vermiculite. Plants were started from seed and thinned to two treatment densities after emergence of cotyledons: 13 pots with 5 seedlings per pot (density of approximately 892 seedlings/m^2) and 26 pots with 15 seedlings per pot (density of approximately 2670 seedlings/m^2), similar to approximate densities previously observed in field plots. Prior to the appearance of the first true leaves on the seedlings, the soil in the pots was watered to field capacity daily. Subsequently, watering was reduced to simulate field drought, and soils were watered to field capacity every three to five days. Soil moisture content or soil water potential measurements were not made. The watering schedule was based on visual observations that the soil was drying out to at least 8-cm depth between watering and that some seedling mortality was occurring. Seedlings in each pot were mapped on a grid, measured for size, and scored for survival at each census.

The second greenhouse study, designated GS2, was conducted to determine relationships between height, aboveground and belowground biomass, and rooting depth. Plants were grown inside the University of Utah greenhouse, during the winter, using metal halide lamps to simulate summer light regimes. Pots of 15-cm-diameter PVC pipe were 31, 61, or 92 cm in height for rooting depth treatments, with 12, 13, and 28 replicate pots, respectively, for the treatments. The bottom of each pot was capped with clear plexiglas so that root growth at the bottom could be observed. Soil mix was the same as in GS1, and holes at the bottom of each pot provided drainage. Plants were started from seed and were grown one to a pot under well-watered conditions with no added nutrients. Plants were harvested if roots were observed at the bottom of a pot on one of the three harvest dates. At harvest, plant heights were recorded and shoot and roots were dried for determination of biomass.

For the 1991–40 and GS1 studies, initial seedling heights were compared for dead versus live categories at each date. A ratio of variances and an F_{max} test were used to determine whether variances were homogeneous for the field study and greenhouse studies (Sokal and Rohlf 1981). For comparisons of two means, Student's *t* tests were used when variances were not different, and approximate Student's *t* tests were used when variances were significantly different (Sokal and Rohlf 1981). For the comparison of seedling height and root biomass as a function of the three rooting depth classes in GS2, variances were unequal, and a Kruskal-Wallis test was used to determine differences among means (Sokal and Rohlf 1981). Comparisons of numbers of seedlings across years were made with Spearman's rank correlation tests (Sokal and Rohlf 1981).

RESULTS

Field Studies

Monthly precipitation patterns varied between years, and of the years studied, only 1991 approached a pattern similar to the 23-year mean (Fig. 1). However, soil moisture patterns for the study years were more consistent, with a reduction in soil moisture that generally began no later than June. Soil moisture was least available in June–July and then increased in August and September. The shallow soil layer (0–35 cm) had a greater seasonal reduction of soil moisture than the deeper soils (35–70 cm) (Fig. 1).

Survival of *C. nauseosus* seedlings was low for all three years monitored, with 0.3, 1.9, and 1.4% for 1989, 1990, and 1991, respectively, surviving the summer (Fig. 1). Seedling censuses started at different times for each of the three years (March until early June), and survival is presented as a percentage of the maximum number of seedlings marked in a given year. For 1991, seedlings were marked as they germinated in March and April, and seedling numbers were greatest in April when most seedlings still had only cotyledons. Seedling mortality that occurred prior to mid-May appeared to be associated with either damping off, freezing damage, or improper rooting (i.e., seedlings that were not securely anchored in the ground and had ≥ 2 cm of root growth visible aboveground). After mid-May, when most seedlings had formed true leaves, seedling mortality appeared to be predominantly due to drought since seedlings dried in place and became brittle and achlorophyllous, with no evidence of herbivory or nutrient limitation.

In the 1991–40 plots, seedling size was monitored throughout the season, and though many seedlings succumbed to the drought, the surviving seedlings grew larger through the season (Fig. 2). For each sampling date, seedlings were grouped into live and dead categories to compare initial heights for

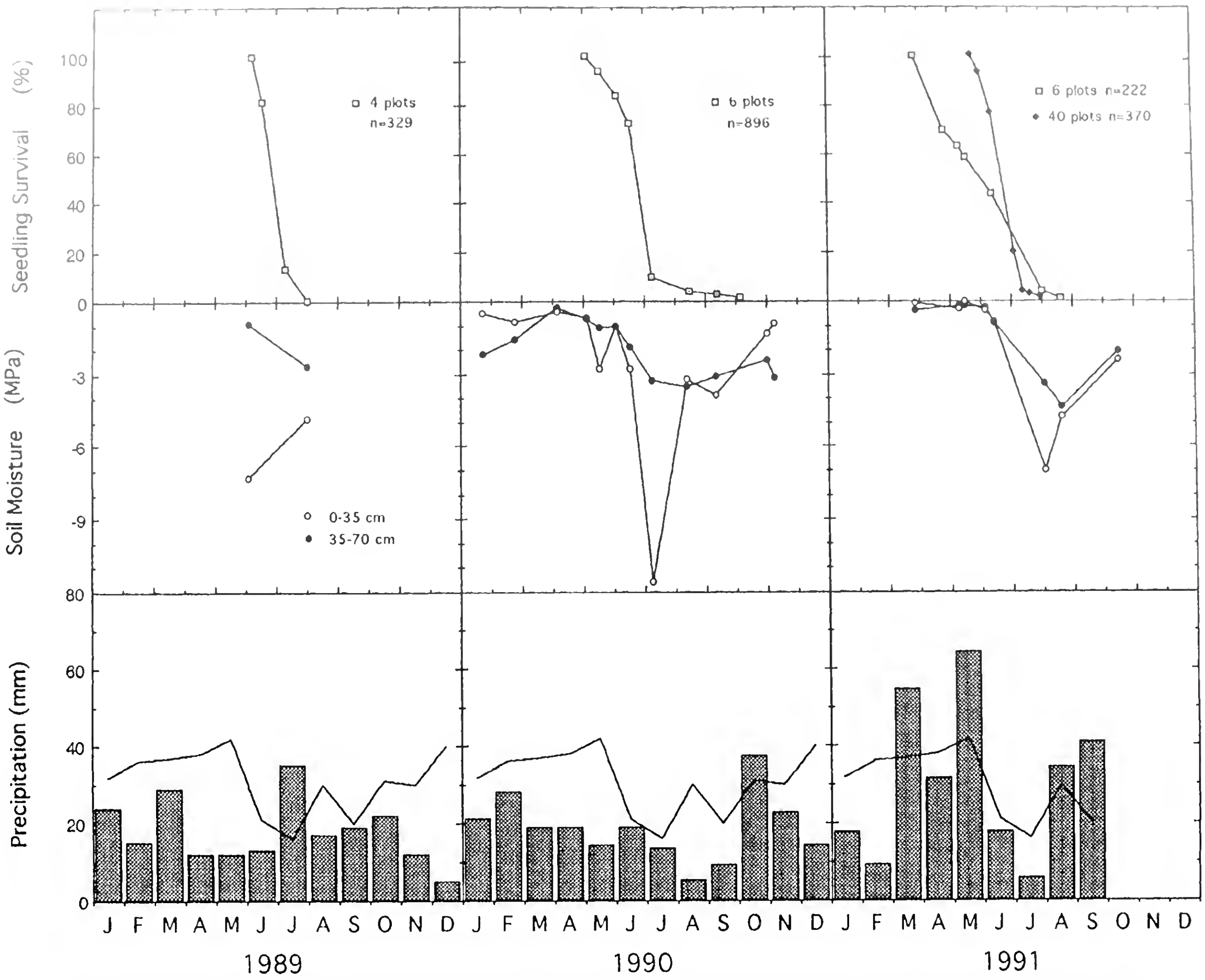

Fig. 1. Seedling survival, soil moisture, and precipitation (bar graph) for *Chrysothamnus nauseosus* at Tintic, Utah, for 1989–91. Solid line in precipitation panel indicates 23-year mean.

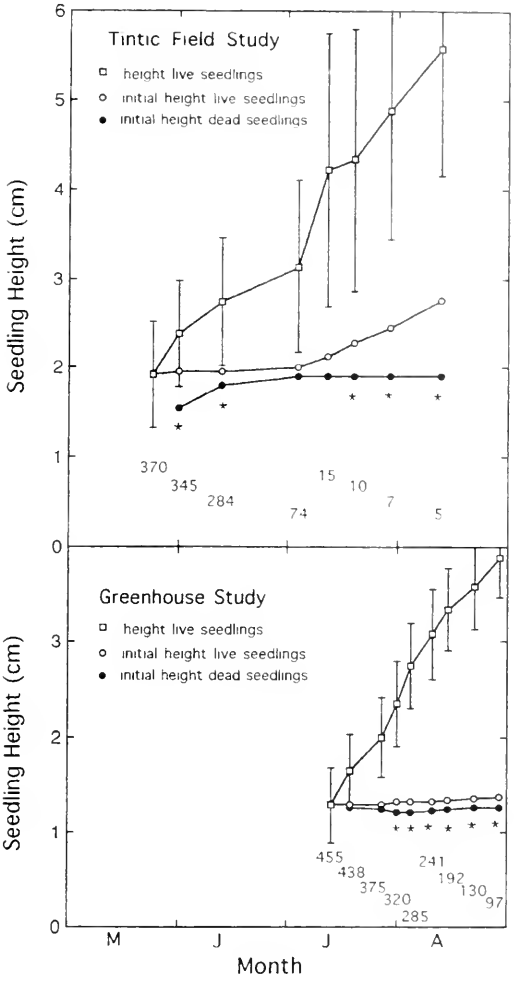

Fig. 2. Height of live seedlings (bars = sd) and initial size of seedlings in alive and dead categories for the Tintic field study and for the greenhouse study. An * along the x axis indicates that initial size for surviving seedlings is significantly greater than the initial size for dead seedlings at that date, $P < .05$. Numbers along x axis indicate number of seedlings alive at each census date.

seedlings in these categories. For most of the sampling dates surviving seedlings had been initially larger (in May) than those that died (Fig. 2). Though the significant differences between the mean initial heights (for subsequent surviving and dead classes) were as small as only 0.1 cm on some dates, the 5 seedlings alive at the end of the study had an initial mean height of 2.7 cm, which was 0.8 cm taller than the mean for the 365 seedlings that had died during the course of the study. To analyze the effect of seedling height throughout the season, we categorized heights of seedlings alive on each date by whether or not they were alive on the next sampling date. *T* tests (one-tailed) indicate that taller seedlings at any date tended to be more likely to survive until the following census date (P = .07, .001, .04, .18, .11, and .09 for the last six field sampling dates).

Spatial distribution of seedlings was examined for the 1991–40 plots. For the 20 randomly distributed plots, seedling numbers within plots averaged 11.8 ± 17.5, with a range of 0–75 (maximum of 625 seedlings m^{-2}). The distance of seedling plots to nearest reproductively mature neighbor averaged 1.1 ± 0.25 m, with a range of 0.3–5.0 m. For these randomly distributed plots, the number of seedlings per plot was not significantly correlated with the distance from the plot to nearest mature neighbor ($n = 20$, $r = .173$, $P > .05$). For the 20 plots systematically oriented within 0.5 m of mature shrubs, numbers of seedlings averaged 7.8 ± 11.4, with a range of 0–41, which was not significantly different from the numbers of seedlings in the random plots ($t = 0.85$, df = 38, $P = .1$). However, when the nonrandomly located plots were categorized on the basis of compass orientation, plots located on the north side of the shrub had significantly more seedlings (21.8) than plots located to the east (5.0), west (2.8), and south (1.8) of the large, mature shrubs ($F = 6.07$, df = 3, $P = .006$).

The distance to nearest seedling neighbor averaged 3.6 ± 3.8 cm and ranged from 0.1 to 29.3 cm for 1991–40 plots that contained at least two seedlings. The initial distance to nearest neighbor was not correlated with seedling height at the initiation of the study or at any subsequent census date during the study ($P > .05$ for all correlation coefficients). When seedlings were categorized by live and dead on each date, there were no differences in initial distance to nearest neighbor for these categories ($P > .05$ for all t-test comparisons), indicating that seedlings with closer neighbors were not more likely to die on subsequent dates. Hence, distance to nearest seedling neighbor had no effect on size or survival in the field plots.

The four plots monitored continuously for three years were ranked for total numbers of seedlings and for number of seedlings alive on 6 June (to reduce the effect of having started the censuses at different times each year). For both total seedling number and number alive in early June, the ranking of the four plots was not consistent across years (Table 1). The total number of seedlings in these four plots ranged from a low of 131 in 1991 to a high of 406 in 1990.

Greenhouse Studies

For GS1 the soil drying resulted in the same type of mortality pattern as observed in the field, though it was displaced by a month since the GS1 drying did not begin until July (Fig. 2). For this study, because seedling size and percentage of seedlings dead on any date did not differ significantly for the density treatments, treatments were combined for all subsequent analyses. The surviving seedlings ($n = 97$) grew to a mean height of 3.9 ± 0.4 cm by the end of the study. For most of the census dates a comparison of initial sizes for dead versus live seedlings indicated that seedlings surviving to that date were initially larger than those that died (Fig. 2). The distance to nearest seedling neighbor averaged 1.7 ± 1.2 cm, with a range of 0.3–8.2 cm. Similar to the results of the field study, there were no differences in initial distance to nearest neighbor for seedlings categorized as live and dead on each date ($P > .05$ for all t-test comparisons). The initial distance to nearest seedling neighbor was not correlated with seedling height at the initiation of the study nor with seedling height on any subsequent sampling date ($P > .05$ for all correlation coefficients).

In GS2 seedlings were grown individually in pots under well-watered conditions. Plant height increased with increased rooting depth (Kruskal-Wallis statistic = 25.6, df = 2, $P < .001$), though there was variation within each of the rooting-depth classes (Fig. 3). For the 30-, 60-, and 90-cm rooting-depth classes, the average seedling heights were 5.4, 8.2, and 16.7 cm, respectively, but the minimum seedling heights were much more similar, 2.5, 2.0, and 3.5 cm, respectively. The relationship between plant height and rooting depth was mediated through the relationships of rooting depth and root biomass (Fig. 3; Kruskal-Wallis statistic = 20.8, df = 2, $P < .001$), root biomass and shoot biomass (Fig. 4, $r = .89$, $n = 53$, $P < .001$), and shoot biomass and height (Fig. 4, $r = .91$, $n = 53$, $P < .001$). Due to these significant associations between plant height, biomass, and rooting depth, small differences in plant height and biomass may have indicated large increases in rooting depth.

TABLE 1. Number of *Chrysothamnus nauseosus* seedlings alive in plots 1–4 for 1989 through 1991 at Tintic, Utah; maximum number marked and (number alive on 6 June).

Plot #	1989 # seedlings	1990 # seedlings	1991 # seedlings
1	96 (96)	387 (235)	43 (37)
2	50 (50)	0 (0)	13 (1)
3	44 (44)	29 (14)	20 (10)
4	139 (139)	48 (6)	55 (29)
total	329 (329)	406 (225)	131 (77)

DISCUSSION

Annual rates of seedling recruitment were low for the *C. nauseosus* population at the Tintic study site. For each year monitored, less than 2% of the marked seedlings survived through the growing season, and the 1989 and 1990 estimates may have erred on the high side since seedlings were not marked until after some mortality had already taken place. In all three years seedling mortality coincided with the progressive declines in soil moisture and appeared to be a result of water stress. These low rates of seedling survival can be compared to estimates of yearly survival for other life history classes of *C. nauseosus* at the same site during the same time period: 83% for 1-year-old juveniles, 98–100% for juveniles greater than 2 years old, and 100% for small and large reproductive plants (Donovan unpublished). The low seedling survival and the timing of mortality for *C. nauseosus* are consistent with those reported for *A. tridentata* at this same field site (Owens 1987).

For both the field and the greenhouse studies, seedlings that survived the drought had initially been taller by only a few millimeters. For the field study there was also a trend for the tallest seedlings on any census date to be more likely to be alive on the following date, though this was not observed in the greenhouse drought study, where the range of heights was much smaller and hence statistically significant differences would be more difficult to obtain. Based on the greenhouse study where seedlings were harvested, the

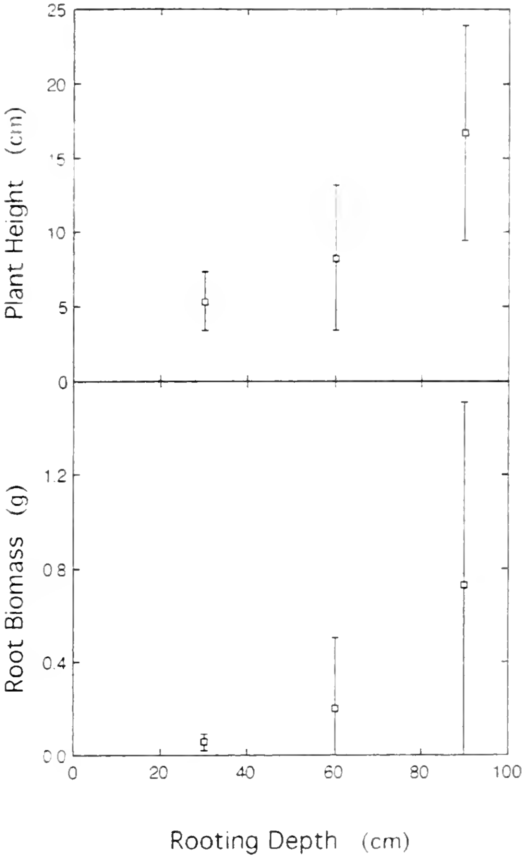

Fig. 3. Plant height and root biomass (mean and sd) as a function of rooting depth for *Chrysothamnus nauseosus* plants grown individually in pots under well watered conditions.

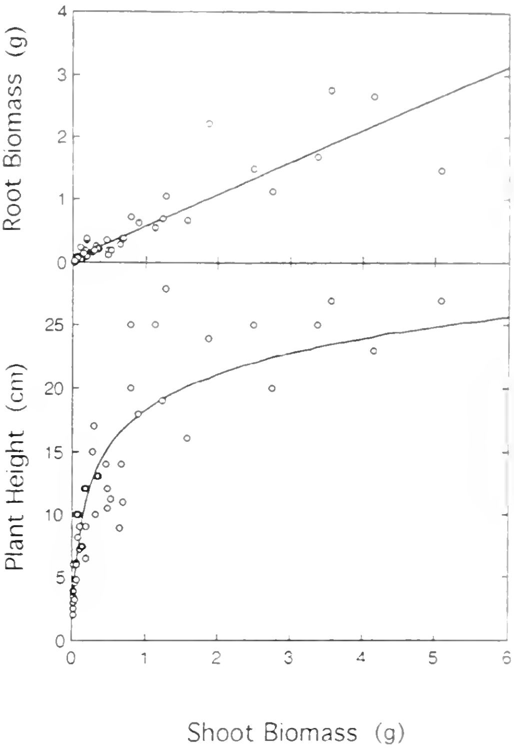

Fig. 4. Relationship of shoot biomass to root biomass ($y = 0.07 + 0.51x$, $r = .89$, $n = 53$, $P < .001$) and to plant height ($y = 18.3 + (9.53 * \log x)$, $r = .91$, $n = 53$, $P < .001$) for *Chrysothamnus nauseosus* seedlings grown individually in pots under well-watered conditions (same plants as in Fig. 3).

taller seedlings had more root biomass and deeper roots, and hence increased access to deeper soil moisture reserves. While greenhouse seedlings had 43% of their biomass belowground, there are no equivalent estimates for seedlings of other Great Basin shrubs. Mature Great Basin shrubs are known to have 65–90% of their biomass belowground (Caldwell 1985, Dobrowolski et al. 1990). Since the greenhouse biomass study was conducted under well-watered conditions, it may have altered the biomass relationships somewhat because drought can result in greater investment in roots (Kozlowski et al. 1991).

The distance to nearest seedling neighbor was not related to survival in either the field or the greenhouse study. It is perhaps surprising that higher seedling densities and closer seedling neighbors did not result in greater competition-induced water stress and hence have an impact on survival. For the field, the lack of an effect of distance to neighbor or density, on either seedling size or survival, may have been associated with patchiness or abiotic microsite characteristics, as well as variable biotic interactions with annual and perennial grasses, forbs, and large shrubs (Fowler 1984, 1986, Reichenberger and Pyke 1990). In the greenhouse there were no other competitors and the microenvironment was uniform, but seedling size and survival were still not affected by seedling density or initial distance to nearest seedling neighbor. The greenhouse densities may have been insufficient to cause a detectable effect, or alternatively, the effects may have been from the interaction of many neighbors and not just the closest one (Fowler 1984).

Though the mechanisms leading to the differences in size were not directly assessed in this study, they have important implications for the patterns resulting from the differential mortality. Seedling size variation may be due to differences in seed size, time of germination, microsite characteristics (abiotic and biotic), and genotypically controlled differences in growth rates (Cook 1980, Fowler 1984, Fenner 1985, Meyer et al. 1989). Since the greenhouse study used seeds collected from mature individuals at the Tintic site, the greenhouse and field studies had similar ranges of seed sizes and seedling genotypes. In the greenhouse studies, seeds were planted at the same time under common conditions and varied relatively little in seedling size at the initiation of the study when most plants had produced the first true leaves. In comparison, the seedlings in the field exhibited greater variation in seedling size, and this may be attributed to greater variation in germination time, abiotic microsite characteristics, and biotic interactions with neighbors (Cook 1980, Fowler 1984, 1986, Owens 1987, Meyer et al. 1989, Reichenberger and Pyke 1990). Regardless of the source of variation in size, it appears that greater seedling size at the beginning of a drought increases access to soil moisture and hence the probability of surviving through the drought. The size-dependent mortality found in our study is consistent with the findings by Cook (1980) that early germinating seedlings of *Viola blanda* were larger and more likely to survive through three successive years, though the cause of mortality in that study was not specified. The high rates of mortality indicate strong potential selection for traits associated with larger seedling size (Cook 1979).

Recruitment of seedlings into the natural population of *C. nauseosus* did not appear to be limited by seed availability or safe sites for germination, since large numbers of seedlings were found even in the dry years of the study. The variation in seedling densities, both spatially and between years, seems to be a common feature of arid and semiarid systems (Mott 1979, Went 1979, West et al. 1979, Owens 1987). The pattern of greater numbers of seedlings germinating on the north side of mature shrubs may be due to greater numbers of seeds or greater availability of safe sites appropriate for germination. Seedling survival may also be enhanced on the north sides of shrubs due to more available soil moisture due to either increased water capability from later snowmelt or decreased water loss (i.e., decreased solar input and increased litter layer), but too few seedlings survived to test this idea. For seedlings in arid and semiarid habitats, large neighbors have been variously described as affecting the seedling survival as beneficial nurse plants or as disadvantageous competitors (Jordan and Nobel 1979, Owens 1987, Reichenberger and Pyke 1990).

Our studies, conducted during two dry years (1989 and 1990) and an average year (1991), indicate that seedling recruitment can be active in a mature population of *C. nauseosus* during most years. Of course, seedling recruitment would be expected to be greater in wetter years when fewer seedlings are lost to drought stress (Ackerman 1979, West et al. 1979, Owens 1987). Rates of recruitment into mature populations may also differ from those into newly disturbed habitats, such as post-fire or chained areas (Young and Evans 1974). However, given that the summer decline in soil moisture is an overriding feature in the Great Basin, larger seedlings with deeper roots may have a greater probability of survival in most years and in most habitats.

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[illegible] AND ABUNDANCE OF BIRDS IN THE [illegible] MOUNTAINS, CALIFORNIA

[illegible]

[illegible] distribution and abundance [illegible] birds in the piñon-juniper and bristlecone-limber pine forests, and (2) quantify [illegible] differences in bird numbers and [illegible] within and between the two forest types.

STUDY AREA

The White Mountains are a [illegible] in length [illegible] immediately [illegible] central Sierra Nevada and Owens [illegible] with [illegible] Mountain Peak—at 4342 m elevation—[illegible] highest point in the Great Basin. [illegible] the rain shadow [illegible] the Sierra Nevada. The mountains are pre[illegible] from 1200 to 2000 [illegible] woodland from 2000 [illegible] pine forest [illegible] alpine zone is pres[illegible] Spira 1991). The similar [illegible] Inyo Mountains continue south from the White Mountains (see Nelson et al. [1991] for further geologic description of these ranges).

Our general study area ran from the northern terminus of the Inyo Mountains near Waucoba and Westgard passes (Inyo County), elevation 2100 m, north for about 30 km into the central White Mountains near the Patriarch Grove (Mono County), elevation 3500 m. The study area was divided into two distinct vegetative zones. The pinyon-juniper zone was dominated by single-leaf pinyon (*Pinus monophylla*), with scattered individuals of Utah juniper (*Juniperus osteosperma*). The understory was predominantly sagebrush (*Artemisia nova* and *A. tridentata*) and bitterbrush (*Purshia tridentata* and *P. glandulosa*), with scattered ephedra (*Ephedra* spp.) and rabbitbrush (*Chrysothamnus* spp.).

The bristlecone–limber pine (or subalpine) zone was dominated by mixtures of these two tree species (Lloyd and Mitchell 1973). The major understory plants were sagebrush, with scattered rabbitbrush and fern bush (*Chamaebatiaria millefolium*). On dry slopes at lower elevations of this zone, pure stands of mountain mahogany (*Cercocarpus ledifolius*) were present. Plant communities of the White Mountains are described in detail by Lloyd and Mitchell (1973) and Spira (1991).

METHODS

Data were collected during the early to middle period of the breeding season of most birds in the Whites (Hall et al. 1991). Counts were conducted from about 1–30 May in the pinyon-juniper zone, and from about 1–30 June in the bristlecone–limber pine zone. We did not confirm that all species observed actually bred. Therefore, our data should be interpreted as consisting of birds observed during the potential spring breeding period.

Transect Establishment

Birds were counted at fixed points along transects. Ten transects were approximately evenly distributed through each vegetation zone, with the exact beginning location determined by selecting a random distance (between 30 and 150 m) and direction (random compass spin) from a convenient access point (secondary or tertiary road). Transects were about 1 km apart within each zone. Unless interrupted by an impassable obstacle, transects ran for 1500 m, then turned left or right (randomly chosen unless terrain dictated otherwise) 90°, ran for 600 m, and then turned back 90° toward the starting point, paralleling the outgoing line. Each transect was thus about 4.2 km long, for a total of about 42 km of transect per vegetation zone. Bird counting points were established every 300 m starting at the beginning of the transect, for a total of 15 points per transect and 150 points per vegetation zone.

Bird Counts

Birds were counted at each point for 10 minutes by each of three observers; thus, each point was counted three times per year, for a total of 450 counts per vegetation zone per year. The same observers counted each year, and all were well acquainted with species by calls and songs. Counting started about sunrise and lasted approximately 4 hours, during which time an observer could count at all 15 points on a transect. Observers reversed the order that points on a transect were counted to compensate for possible temporal variation in bird activity during a morning. All birds seen or heard within the 10-minute period were recorded regardless of distance from the point so that a complete listing of birds could be made. Observers attempted to avoid double-counting birds during a count and between points. For this paper, data are pooled by sex, and all detection modes (visual, singing, calling) were used. Too few species were sexually dichromatic or dimorphic to differentiate sex in the field, and many detections were made by call note.

Data Analysis

An index of abundance was calculated for each point per year as the average number of detections per count ($\bar{x} \pm$ SD, n = 3 counts/point). These mean point values were then averaged for each vegetative zone (n = 150 points/year).

One-way analysis of variance (ANOVA) was used to test for overall significant ($P < .05$) differences in total bird and individual species abundances among years for each vegetative zone. Where the ANOVA was significant, Scheffe's procedure was used to identify which years differed ($P \leq .05$) from each other in abundance (Zar 1984:196–198). Count data were normally distributed or nearly so; thus, no data transformations were necessary because of the robust nature of ANOVA (Zar 1984:169–170). Power of the ANOVAs was determined a posteriori by selecting several species based on their overall abundance (i.e., rare or common) for testing. This analysis indicates the chance of having committed a Type II error and is especially relevant for rare species where the null hypothesis of no difference in abundance among years was not rejected. That is, how confident are we that abundance is indeed not declining? Procedures followed Zar (1984:174) for power of a performed test.

Spearman's rank correlation (Zar 1984: 318–320) was used to determine the degree of similarity in bird species composition and abundance between vegetative zones among years. To eliminate the influence of extremely rare occurrences, only species for which >100 individuals were detected over the 3 years combined (for each vegetation type) were included in this analysis. Thus, only the very rare species were excluded from this analysis.

T tests were used to compare total bird abundance between vegetation zones within each year and pooled over all 3 years.

RESULTS

Species Composition and Abundance

PINYON-JUNIPER ZONE.—Overall (all years combined), 58 potentially breeding species were encountered in the pinyon-juniper zone. The number of species detected declined across years: 53, 49, and 45 for 1989–91, respectively (Table 1). The ranking of species by their abundances (very rare species excluded) was similar among years (all $r_s > .78$, $P < .01$; Table 2).

The pinyon-juniper zone was characterized by a few very abundant species (index ≥ 1.0, 3 species), a few moderately abundant species (index ≥ 0.25–0.99, 5 species—only 1 species was at ≥ 0.25–0.49), a larger number of common to uncommon species (index ≥ 0.1–0.24, 11 species), and numerous rare species (index ≤ 0.1, 41 species; Tables 1 and 2). Overall, the Black-throated Gray Warbler was the most abundant bird—it ranked first in abundance in 2 of 3 years. The Gray Flycatcher and Pinyon Jay were the next most abundant species, ranking in the top three in all years (Table 2).

The Bewick's Wren, Mountain Chickadee, Chipping Sparrow, Bushtit, and Rock Wren were, with one exception (Rock Wren in 1990), always among the top 10 birds by abundance. The remaining species with indices ≥ 0.1 complete the list of predominant species in this zone. Note that the nest parasite, the Brown-headed Cowbird, was the ninth most abundant species (Table 2). Eighteen potentially breeding species were not present in 1 or 2 years—all were rare in overall abundance (Table 1).

Total abundance was nearly identical for 1989 and 1991; abundance in 1990 was significantly higher. The Black-throated Gray Warbler, Pinyon Jay, and Bewick's Wren—three of the four most abundant species—had substantially higher counts in 1990 (Table 1). Further, several relatively uncommon species overall (e.g., Cassin's Finch, Clark's Nutcracker) were detected more in 1990.

Twenty-two species showed significant inter-year variations in abundance; however, only six of these species had overall indices ≥ 0.25. Significant declines in abundance across all years, or for 2 adjacent years followed by no increase in the third, were seen for eight species (the Northern Pygmy Owl was excluded): Blue-gray Gnatcatcher, Black-throated Sparrow, Common Raven, Mountain Chickadee, Northern Flicker, Rufous-sided Towhee, Scrub Jay, and White-breasted Nuthatch (Table 1). Significant increases were seen for five species: Bushtit, Gray Flycatcher, Green-tailed Towhee (very rare, overall index = 0.01), Rock Wren, and Violet-green Swallow. The remaining species with significant inter-year variation had their highest observed abundances in 1990 (Table 1).

Bristlecone–Limber Pine Zone

Overall, 61 species were observed in the bristlecone–limber pine zone. The number of species was highest in 1990 (54 species) and slightly lower in 1989 (50) and 1991 (51) (Table 3). The ranking of species by abundance (very rare species excluded) was similar among years (all $r_s > .71$, $P < .01$; Table 4).

This zone was characterized by few very abundant species (index ≥ 1.0, 3 species), a few moderately abundant species (index ≥ 0.25–0.99, 7 species), only a few common (index ≥ 0.25–0.49, 5 species) to uncommon species (index ≥ 0.1–0.24, 5 species), and

TABLE 1. Indices of abundance for birds in the pinyon-juniper zone, White Mountains, California, spring 1989-91

	1989		1990		1991			1989–91	
Species	$\bar{x}$	SD	$\bar{x}$	SD	$\bar{x}$	SD	P	$\bar{x}$	SD
Northern Goshawk (*Accipiter gentilis*)	<0.01	0.03	NP[b]		<0.01	0.05	.607	0.00	0.02
Red-tailed Hawk (*Buteo jamaicensis*)	0.02	0.08	<0.01	0.04	0.01	0.07	.094	0.01	0.06
Golden Eagle (*Aquila chrysaetos*)	<0.01	0.03	NP		NP		.369	0.00	0.02
American Kestrel (*Falco sparverius*)	0.02	0.11	<0.01	0.01	<0.01	0.05	.191	0.01	0.07
Mountain Quail (*Oreortyx pictus*)	<0.01A	0.03	0.03B	0.12	NP A		.002	0.01	0.07
Mourning Dove (*Zenaida macroura*)	0.02	0.13	0.02	0.10	0.02	0.08	.955	0.02	0.10
Great-horned Owl (*Bubo virginianus*)	<0.01	0.03	NP		NP		.369	0.00	0.02
Northern Pygmy-Owl (*Glaucidium gnoma*)	0.01B	0.08	NP A		NP A		.010	0.00	0.04
White-throated Swift (*Aeronautes saxatalis*)	0.02	0.11	0.01	0.05	<0.01	0.03	.061	0.01	0.07
Broad-tailed Hummingbird (*Selasphorus platycercus*)	0.04	0.13	0.02	0.08	0.05	0.12	.092	0.04	0.11
Northern Flicker (*Colaptes auratus*)	0.09B	0.16	0.04A	0.12	0.04A	0.13	.001	0.05	0.14
Red-breasted Sapsucker (*Sphyrapicus ruber*)	<0.01	0.03	NP		NP		.369	0.00	0.02
Hairy Woodpecker (*Picoides villosus*)	0.03	0.12	0.02	0.07	0.03	0.09	.122	0.02	0.09
Downy Woodpecker (*Picoides pubescens*)	<0.01	0.03	NP		NP		.369	0.00	0.02
Ash-throated Flycatcher (*Myiarchus cinerascens*)	0.21	0.29	0.20	0.37	0.18	0.32	.658	0.20	0.33
Say's Phoebe (*Sayornis saya*)	<0.01	0.03	NP		NP		.369	0.00	0.02
Dusky Flycatcher (*Empidonax oberholseri*)	0.01	0.05	0.02	0.09	0.02	0.10	.082	0.02	[illegible]
Gray Flycatcher (*Empidonax wrightii*)	1.15B	0.62	1.67A	0.81	1.68A	0.82	.000	1.50	[illegible]
Western Wood-Pewee (*Contopus sordidulus*)	<0.01	0.04	0.02	0.08	0.02	0.07	.068	0.01	0.06
Olive-sided Flycatcher[c] (*Contopus borealis*)	NP		NP		<0.01	0.05	.369	0.00	0.02

[illegible] Continued.

Species	1989 $\bar{x}$	1989 SD	1990 $\bar{x}$	1990 SD	1991 $\bar{x}$	1991 SD	P^a	1989–91 $\bar{x}$	1989–91 SD
Horned Lark (*Eremophila alpestris*)	<0.01	0.03	NP		0.03	0.41	.394	0.01	0.24
Bewick's Wren (*Thryomanes bewickii*)	0.84A	0.18	1.05B	0.59	0.73A	0.52	.000	0.87	0.55
Canyon Wren (*Catherpes mexicanus*)	NP A		0.02B	0.10	0.01A	0.06	.007	0.01	0.07
Rock Wren (*Salpinctes obsoletus*)	0.24A	0.32	0.26A	0.34	0.49B	0.52	.000	0.33	0.42
American Robin (*Turdus migratorius*)	NP		0.01	0.05	NP		.049	0.00	0.03
Hermit Thrush (*Catharus guttatus*)	<0.01	0.03	<0.01	0.03	0.01	0.07	.323	0.00	0.04
Mountain Bluebird (*Sialia currucoides*)	0.17	0.30	0.26	0.34	0.20	0.03	.072	0.21	0.33
Townsend's Solitaire (*Myadestes townsendi*)	<0.01	0.04	<0.01	0.03	NP		.367	0.00	0.03
Blue-gray Gnatcatcher (*Polioptila caerulea*)	0.20A	0.32	0.13B	0.25	0.06C	0.15	.000	0.13	0.26
Ruby-crowned Kinglet[c] (*Regulus calendula*)	NP B		0.04A	0.12	0.04A	0.12	.000	0.03	0.10
Solitary Vireo (*Vireo solitarius*)	0.09	0.19	0.11	0.25	0.07	0.16	.175	0.09	0.21
Orange-crowned Warbler[c] (*Vermivora celata*)	NP		<0.01	0.04	NP		.135	0.00	0.02
Yellow-rumped Warbler (*Dendroica coronata*)	NP		0.02	0.22	<0.01	0.04	.291	0.01	0.13
Black-throated Gray Warbler (*Dendroica nigrescens*)	1.77A	0.67	1.98B	0.79	1.41C	0.72	.000	1.73	0.76
Townsend's Warbler[c] (*Dendroica townsendi*)	0.01	0.06	0.01	0.08	<0.01	0.03	.447	0.01	0.06
MacGillivray's Warbler (*Oporornis tolmiei*)	<0.01	0.03	0.01	0.07	NP		.071	0.00	0.04
Wilson's Warbler (*Wilsonia pusilla*)	0.01	0.06	0.03	0.11	0.01	0.08	.151	0.02	0.09
Scott's Oriole (*Icterus parisorum*)	0.03	0.12	0.04	0.11	0.04	0.11	.897	0.03	0.13
Northern Oriole (*Icterus galbula*)	<0.01	0.03	NP		NP		.369	0.00	0.02
[illegible]	[illegible]	[illegible]	0.27A	0.19	0.26A	0.16	.019	0.23	0.42

TABLE 1. Continued.

	1989		1990		1991			1989–91	
Species	$\bar{x}$	SD	$\bar{x}$	SD	$\bar{x}$	SD	P^a	$\bar{x}$	SD
Western Tanager (*Piranga ludoviciana*)	0.02	0.09	0.06	0.21	0.04	0.17	.169	0.04	0.16
Black-headed Grosbeak (*Pheucticus melanocephalus*)	0.09	0.19	0.04	0.14	0.06	0.23	.103	0.07	0.19
Purple Finch[c] (*Carpodacus purpureus*)	0.01	0.05	0.01	0.05	NP		.219	0.00	0.04
Cassin's Finch (*Carpodacus cassinii*)	0.15A	0.30	0.28B	0.42	0.16A	0.39	.003	0.20	0.38
House Finch (*Carpodacus mexicanus*)	0.23A	0.34	0.16A	0.31	0.27B	0.44	.028	0.22	0.37
Lesser Goldfinch (*Carduelis psaltria*)	<0.01A	0.04	0.05B	0.18	NP A		.000	0.02	0.11
Green-tailed Towhee (*Pipilo chlorurus*)	<0.01A	0.03	0.02AB	0.09	0.02B	0.08	.031	0.01	0.07
Rufous-sided Towhee (*Pipilo erythrophthalmus*)	0.28B	0.40	0.11A	0.22	0.05A	0.17	.000	0.14	0.30
Lark Sparrow (*Chondestes grammacus*)	0.02	0.11	<0.01	0.04	NP		.054	0.01	0.07
Black-throated Sparrow (*Amphispiza bilineata*)	0.14A	0.28	0.06B	0.22	0.01B	0.07	.000	0.07	0.21
Dark-eyed Junco (*Junco hyemalis*)	0.03	0.12	0.03	0.10	0.05	0.17	.309	0.04	0.13
Chipping Sparrow (*Spizella passerina*)	0.49	0.49	0.58	0.50	0.50	0.45	.196	0.52	0.48
Brewer's Sparrow (*Spizella breweri*)	NP		NP		<0.01	0.03	.369	0.00	0.02
White-crowned Sparrow[c] (*Zonotrichia leucophrys*)	<0.01	0.03	NP		NP		.369	0.00	0.02
Violet-green Swallow (*Tachycineta thalassina*)	0.03A	0.11	0.14B	0.43	0.11AB	0.15	.019	0.09	0.27
Tree Swallow (*Tachycineta bicolor*)	NP		0.01	0.08	NP		.369	0.00	0.05
Steller's Jay[c] (*Cyanocitta stelleri*)	<0.01	0.04	NP		NP		.155	0.00	0.02
Scrub Jay (*Aphelocoma coerulescens*)	0.19A	0.28	0.11A	0.24	0.07B	0.16	.000	0.13	0.24
Common Raven (*Corvus corax*)	0.08A	0.21	0.06A	0.18	0.02B	0.08	.006	0.05	0.17
Pinyon Jay (*Gymnorhinus cyanocephalus*)	1.08	2.29	1.72	3.44	1.27	1.81	.089	1.36	2.61

TABLE [illegible]. Continued.

	1989		1990		1991			1989–91	
Species	$\bar{x}$	SD	$\bar{x}$	SD	$\bar{x}$	SD	P[a]	$\bar{x}$	SD
Clark's Nutcracker *Nucifraga columbiana*	0.12A	0.27	0.20B	0.31	0.07A	0.23	.000	0.13	0.27
Mountain Chickadee *Parus gambeli*	0.65A	0.63	0.61A	0.59	0.46B	0.55	.012	0.57	0.59
Plain Titmouse *Parus inornatus*	0.18	0.29	0.21	0.29	0.25	0.33	.179	0.21	0.30
Bushtit *Psaltriparus minimus*	0.40A	0.46	0.51AB	0.69	0.61B	0.64	.011	0.51	0.61
White-breasted Nuthatch *Sitta carolinensis*	0.19A	0.29	0.15A	0.23	0.07B	0.14	.000	0.14	0.24
Fox Sparrow *Passerella iliaca*[c]	0.01	0.07	<0.01	0.00	0.01	0.09	.170	0.01	0.06
Unknown	0.11A	0.21	0.10A	0.21	0.05B	0.14	.025	0.09	0.19
Total	9.69A	4.83	11.61B	6.44	9.63A	4.53	.001	10.31	5.41

[a] P associated with ANOVA of yearly data. When $P < .05$, years with like letters were not significantly different based on Scheffe's procedure.

[b] NP = not present

[c] Nonbreeding species in our study area

numerous rare species (index ≤ 0.1, 41 species) (Tables 3 and 4). Overall, Clark's Nutcracker was the most abundant bird—it ranked first in abundance in 2 of 3 years. The Mountain Chickadee was first or second in abundance over the 3 years. The third most abundant species overall—the Cassin's Finch—actually ranked fourth and fifth in 2 years (Table 4).

The Dusky Flycatcher, Violet-green Swallow, Pygmy Nuthatch, Green-tailed Towhee, and Mountain Bluebird ranked in the top 10 in abundance for all 3 years. The Gray Flycatcher and Rock Wren each ranked in the top 10 overall and for 2 of 3 years but were relatively low in 1989. The remaining species with indices >0.1 (abundance ranks 10–20) were relatively consistent in their rankings across years (Table 4). Eighteen potentially breeding species were not present during 1 or 2 years; all were rare in overall abundance (Table [illegible]).

Total abundance declined slightly across years, with 1989 being significantly greater than 1990–91 (Table [illegible]). Twenty-one species showed significant interyear variations in abundance; this included [illegible] relatively rare (index <0.05) species, 8 of which showed declines (Table 3). Species with overall abundances >0.10 that showed significant declines were Cassin's Finch, Dusky Flycatcher, Hermit Thrush, Mountain Chickadee, Northern Flicker, Pygmy Nuthatch, and White-breasted Nuthatch. Significant increases were shown for the Gray Flycatcher and Rock Wren (Table 3).

Comparisons Between Vegetation Zones

Total bird abundance was significantly greater (P <.001, t tests) in the bristlecone–limber pine zone compared to the pinyon-juniper zone in 1989 and 1991; no significant difference (P = .15) existed in 1990. Overall (1989–91) total abundance was significantly greater (P < .001, t test) in the bristlecone–limber pine zone (compare Tables 1 and 3).

Forty-five species potentially bred in both zones; however, only 10 of these species had abundance indices of >0.1 in both zones, and 21 species were rare (index <0.1) in both zones (Table 5). The Gray Flycatcher, Mountain Chickadee, and Rock Wren were in the top 10 in abundance in each zone; the Black-throated Gray Warbler, Cassin's Finch, Chipping

TABLE 2. Ranking of relatively abundant (index ≥ 0.1 overall) species by year in the pinyon-juniper zone, White Mountains, California, 1989–91.

	Ranking by year		
Overall ranking[a]	1989	1990	1991
Index ≥ 1.0			
1. Black-throated Gray Warbler	1	1	2
2. Gray Flycatcher	2	3	1
3. Pinyon Jay	3	2	3
Index ≥ 0.5–0.99			
4. Bewick's Wren	4	4	4
5. Mountain Chickadee	5	5	8
6. Chipping Sparrow	6	6	6
7. Bushtit	7	7	5
Index ≥ 0.25–0.49			
8. Rock Wren	9	11	7
Index ≥ 0.1–0.24			
9. Brown-headed Cowbird	17	9	10
10. House Finch	10	16	9
12. Mountain Bluebird	16	11	12
12. Plain Titmouse	15	12	11
14. Ash-throated Flycatcher	11	14	13
14. Cassin's Finch	18	8	14
16. Rufous-sided Towhee	8	21	—[b]
16. White-breasted Nuthatch	14	16	—
19. Blue-gray Gnatcatcher	12	19	—
19. Clark's Nutcracker	20	14	—
19. Scrub Jay	14	18	—

[a] Based on overall 1989–91 count results (Table 1).

[b] Yearly index <0.10 and thus not ranked.

Sparrow, and Mountain Bluebird were in the top 15 in both zones; and the White-breasted Nuthatch ranked 14th and 16th in the two zones (Table 5).

Power analysis indicated that there was little chance (i.e., <5%) of a Type II error having been committed for ANOVAs at $P < .01$. For significant ANOVAs at $.01 < P < .05$, however, chances of a Type II error ranged from 20% to 40%. For ANOVAs that indicated no significant difference among years at $.05 < P < .1$, chances of a Type II error were generally 60–70%.

DISCUSSION

The pinyon-juniper and bristlecone–limber pine zones were nearly identical in total species richness and in distribution of abundance among species. The bristlecone–limber pine zone, however, had a higher overall abundance of birds relative to the pinyon-juniper. Each zone was characterized by possessing a few very abundant to abundant species, but numerous rare species. They differed only in that the pinyon-juniper zone had more species in the uncommon abundance category. The biological significance of this single difference may be negligible, however, especially given that these results were based on our definition of abundance categories (e.g., values of 0.24 and 0.25 are placed in different categories). The top 15–20 species were fairly consistent in ranked abundances across all 3 years.

Only 10 species with overall uncommon or greater abundance potentially bred in both zones; most species present in both zones were rare. The Gray Flycatcher, Mountain Chickadee, and Rock Wren were relatively common in both zones. The Gray Flycatcher was concentrated in and around mountain mahogany stands at the lower elevation of the bristlecone–limber pine, whereas the chickadee and Rock Wren were found throughout both zones (see also Johnson and Cicero 1986, Hall et al. 1991).

Thus, the two zones were largely different in ranking of species by abundance but drew upon the same general pool of species. There were few clear ecological or taxonomic replacements of species between zones. Gray and Dusky flycatchers overlapped in mountain mahogany, but the Gray did not invade the pure bristlecone–limber pine forest. The Black-throated Gray Warbler declined in abundance with elevation and was not replaced by another warbler (the yellow-rumped was rare in bristlecone–limber pine). The Bewick's Wren also declined in abundance with elevation, whereas the Rock Wren was about equally abundant throughout the study area. The White-breasted Nuthatch was scarce throughout both zones, and the Pygmy Nuthatch occurred only in the bristlecone–limber pine forests. Possible cases of ecological replacement were the Rufous-sided Towhee by the Green-tailed Towhee, and the Pinyon Jay by the Clark's Nutcracker.

The difference in number of species among years in the pinyon-juniper zone resulted from rare species (e.g., American Robin, Canyon Wren, Brewer's Sparrow), questionable breeders (e.g., Tree Swallow, Yellow-rumped Warbler), and species for which our count method was not optimal (e.g., owls and hawks) being included in this analysis (Table 1). Among-year variations in species in the [illegible] abundance for birds in the bristlecone–limber pine zone, White Mountains, California, spring 1989–91.

	1989		1990		1991			1989–91	
Species	$\bar{x}$	SD	$\bar{x}$	SD	$\bar{x}$	SD	P[a]	$\bar{x}$	SD
Turkey Vulture[c] (*Cathartes aura*)	<0.01	0.03	NP[b]		NP		.369	0.00	0.02
Sharp-shinned Hawk (*Accipiter striatus*)	NP		<0.01	0.04	NP		.135	0.00	0.02
Red-tailed Hawk	<0.01	0.03	0.01	0.05	0.01	0.05	.412	0.01	0.04
Golden Eagle	<0.01	0.04	NP		NP		.135	0.00	0.02
American Kestrel	0.01	0.05	<0.01	0.05	<0.01	0.04	.891	0.01	0.05
Sage Grouse (*Centrocercus urophasianus*)	NP		0.04	0.42	NP		.224	0.01	0.24
Mountain Quail	NP		<0.01	0.03	NP		.369	0.00	0.02
Mourning Dove	NP		<0.01	0.03	NP		.369	0.00	0.02
Common Poor-will (*Phalaenoptilus nuttallii*)	NP		<0.01	0.03	NP		.369	0.00	0.02
Broad-tailed Hummingbird	0.01	0.07	0.01	0.06	0.01	0.06	.938	0.01	0.06
Northern Flicker	0.27A	0.31	0.22AB	0.27	0.16B	0.26	.003	0.22	0.29
Red-breasted Sapsucker	<0.01	0.03	NP		<0.01	0.03	.607	0.00	0.02
Red-naped Sapsucker (*Sphyrapicus nuchalis*)	0.06B	0.14	<0.01A	0.03	<0.01A	0.03	.000	0.02	0.09
Hairy Woodpecker	0.06A	0.15	0.06A	0.23	0.01B	0.07	.015	0.04	0.17
Downy Woodpecker	<0.01	0.03	NP		<0.01	0.03	.607	0.00	0.02
Say's Phoebe	0.01	0.07	<0.01	0.04	NP		.221	0.00	0.04
Dusky Flycatcher	1.31A	0.70	0.88B	0.69	0.63C	0.51	.000	0.94	0.70
Gray Flycatcher	0.42B	0.46	0.93A	0.63	0.97A	0.57	.000	0.77	0.61
Western Wood Pewee	0.02AB	0.07	0.00A	0.04	0.03B	0.11	.005	0.02	0.08
Olive-sided Flycatcher	0.02	0.07	0.03	0.10	0.02	0.08	.466	0.02	0.08
Horned Lark	0.01	0.10	<0.01	0.04	0.01	0.06	.703	0.01	0.07
Violet-green Swallow	0.74	0.89	0.64	0.71	0.63	0.84	.446	0.67	0.83
[illegible]	NP		0.01	0.07	NP		.069	0.00	0.01
St[illegible]	[illegible]	0.12	NP		<0.01	0.04	.154	0.01	0.07
Scrub J[illegible]	[illegible]	0.12	0.01	0.09	0.01	0.05	.054	0.01	0.09
Common Ra[illegible]	[illegible]	[illegible]	0.02AB	0.10	NP B		.014	0.02	0.09
Pinyon Jay	[illegible]	[illegible]	NP		NP		.182	0.02	0.34

TABLE 3. Continued.

	1989		1990		1991			1989–91	
Species	*x*	SD	*x*	SD	*x*	SD	*P*	*x*	SD
Clark's Nutcracker	1.61A	1.12	1.36A	1.06	2.21B	1.73	.000	1.73	1.47
Mountain Chickadee	1.60A	0.87	1.48A	0.85	1.26B	0.76	.002	1.45	0.84
Plain Titmouse[c]	<0.01	0.01	NP		NP		.135	0.00	0.02
Bushtit	0.02	0.15	0.01	0.15	0.05	0.23	.370	0.04	0.18
White-breasted Nuthatch	0.12A	0.35	0.11A	0.38	0.21B	0.28	.000	0.35	0.36
Red-breasted Nuthatch (*Sitta canadensis*)	NP		0.01	0.05	0.01	0.06	.323	0.00	0.04
Pygmy Nuthatch (*Sitta pygmaea*)	0.77B	0.77	0.46A	0.53	0.17A	0.61	.000	0.57	0.66
Brown Creeper (*Certhia americana*)	0.23	0.30	0.18	0.31	0.18	0.31	.297	0.20	0.31
House Wren (*Troglodytes aedon*)	0.06B	0.16	0.02A	0.09	0.01A	0.05	.000	0.03	0.11
Bewick's Wren	0.13	0.35	0.14	0.41	0.11	0.33	.757	0.13	0.36
Canyon Wren	NP		NP		<0.01	0.03	.369	0.00	0.02
Rock Wren	0.25A	0.44	0.55B	0.57	0.80C	0.74	.000	0.53	0.64
Sage Thrasher (*Oreoscoptes montanus*)	NP		0.02	0.09	0.01	0.05	.081	0.01	0.06
American Robin	0.04	0.15	0.05	0.20	0.01	0.21	.920	0.04	0.19
Hermit Thrush	0.48A	0.58	0.42AB	0.51	0.33B	0.39	.035	0.41	0.50
Mountain Bluebird	0.53	0.50	0.54	0.49	0.44	0.52	.142	0.50	0.50
Townsend's Solitaire	0.05B	0.14	0.02A	0.07	0.03A	0.11	.022	0.03	0.11
Blue-gray Gnatcatcher	0.01	0.06	0.05	0.19	0.01	0.16	.055	0.03	0.15
Ruby-crowned Kinglet	0.06A	0.18	0.02B	0.08	0.01AB	0.14	.035	0.04	0.14
Solitary Vireo	<0.01	0.03	NP		<0.01	0.04	.367	0.00	0.03
Warbling Vireo (*Vireo gilvus*)	NP		0.02	0.11	0.01	0.05	.073	0.01	0.07
Orange-crowned Warbler[c]	<0.01	0.04	NP		NP		.135	0.00	0.02
Nashville Warbler[c] (*Vermivora ruficapilla*)	<0.01	0.03	NP		NP		.369	0.00	0.02
Yellow-rumped Warbler	0.10	0.21	0.09	0.20	0.12	0.22	.556	0.10	0.21
Black-throated Gray Warbler	0.34	0.59	0.40	0.59	0.38	0.51	.695	0.37	0.56
Common Yellowthroat[c] (*Geothlypis trichas*)	NP		NP		<0.01	0.03	.369	0.00	0.02

TABLE 3. Continued.

Species	1989		1990		1991			1989–91	
	$\bar{x}$	SD	$\bar{x}$	SD	$\bar{x}$	SD	P^a	$\bar{x}$	SD
Red-winged Blackbird (*Agelaius phoeniceus*)	<0.01	0.03	NP		NP		.369	0.00	0.02
Brewer's Blackbird (*Euphagus cyanocephalus*)	0.01	0.35	0.03	0.24	0.02	0.15	.797	0.03	0.26
Brown-headed Cowbird	0.02A	0.08	<0.01AB	0.03	0.00B	0.03	.036	0.01	0.05
Western Tanager	0.02	0.08	0.04	0.11	0.03	0.10	.285	0.03	0.10
Black-headed Grosbeak	0.03A	0.10	NP B		0.01A	0.07	.001	0.01	0.07
Cassin's Finch	1.28A	0.78	1.12A	0.87	0.67B	0.74	.000	1.02	0.84
Pine Siskin[c] (*Carduelis pinus*)	<0.01	0.03	NP		NP		.369	0.00	0.02
Red Crossbill (*Loxia curvirostra*)	0.04	0.16	0.11	0.35	0.10	0.35	.113	0.08	0.30
Green-tailed Towhee	0.58	0.89	0.47	0.81	0.61	0.79	.302	0.55	0.83
Rufous-sided Towhee	0.07B	0.21	0.02A	0.10	0.01A	0.05	.000	0.03	0.14
Savannah Sparrow (*Passerculus sandwichensis*)	NP A		0.01B	0.07	NP A		.002	0.00	0.04
Vesper Sparrow (*Pooecetes gramineus*)	0.02	0.13	0.02	0.14	0.04	0.24	.662	0.03	0.18
Dark-eyed Junco	0.46	0.38	0.44	0.44	0.41	0.41	.522	0.44	0.41
Chipping Sparrow	0.25	0.39	0.24	0.38	0.30	0.45	.334	0.26	0.41
Brewer's Sparrow	0.21	0.59	0.20	0.55	0.26	0.63	.639	0.23	0.59
Fox Sparrow	0.15AB	0.38	0.24A	0.45	0.07B	0.18	.000	0.15	0.36
Unknown	0.21B	0.24	0.04A	0.13	0.02A	0.08	.000	0.09	0.18
Total	13.19B	5.05	12.14A	4.35	11.82A	4.46	.001	12.38	4.66

[a][illegible] ANOVA of yearly data. When $P < .05$, years with like letters were not significantly different based on Scheffe's procedure.

[b][illegible]

[c][illegible] species in our study area.

bristlecone-limber pine zone resulted from [illegible] rare (e.g., Canyon Wren, Black-headed Grosbeak) and questionable or sporadic (e.g., Golden Eagle) breeders being included in the [illegible].

It [illegible] the biological significance of [illegible] disappearances of rare species [illegible]. Our sampling method was [illegible] the abundance of species [illegible] distributions (i.e., our random [illegible] missed rare habitat configurations [illegible]-ranging habits (e.g., soaring raptors), and peak activity periods that do not coincide with our counts (e.g., owls, poor-wills). Power analysis indicated that we should have confidence in ANOVAs showing significant differences across years, especially those with highly significant differences. Power also indicated, however, that we should be skeptical of ANOVAs that failed to reject the null hypothesis of no difference among years at $.05 < P < .1$. That is, we cannot be confident that these species did not change in abundance among

TABLE 4. Ranking of relatively abundant (index ≥ 0.1 overall) species by year in the bristlecone–limber pine zone, White Mountains, California, 1989–91.

	Ranking by year		
Overall ranking[a]	1989	1990	1991
Index ≥ 1.0			
1. Clark's Nutcracker	1	2	1
2. Mountain Chickadee	2	1	2
3. Cassin's Finch	4	3	5
Index ≥ 0.50–0.99			
4. Dusky Flycatcher	3	5	7
5. Gray Flycatcher	12	4	3
6. Violet-green Swallow	6	6	7
7. Pygmy Nuthatch	5	10	9
8. Green-tailed Towhee	7	9	8
9. Rock Wren	16	7	4
10. Mountain Bluebird	8	8	10
Index ≥ 0.25–0.49			
11. Dark-eyed Junco	10	11	11
12. Hermit Thrush	9	12	13
13. Black-throated Gray Warbler	13	14	12
14. White-breasted Nuthatch	12	13	16
15. Chipping Sparrow	16	16	14
Index ≥ 0.1–0.24			
16. Brewer's Sparrow	18	18	15
17. Northern Flicker	14	17	18
18. Brown Creeper	17	19	17
19. Fox Sparrow	19	16	—[b]
20. Bewick's Wren	20	20	19

[a] Based on overall 1989–91 count results (Table 3).
[b] Yearly index <0.10 and thus not ranked.

TABLE 5. Species present during spring in both pinyon-juniper and bristlecone–limber pine zones based on overall (1989–91) abundance rankings. Order of species based on total of the two ranks; all rare (<0.1 index) species assigned a ranking of 25 for simplicity.

Species in common	Pinyon-juniper rank	Bristlecone–limber pine rank
Gray Flycatcher	2	5
Mountain Chickadee	5	2
Black-throated Gray Warbler	1	13
Rock Wren	8	9
Cassin's Finch	11	3
Clark's Nutcracker	19	1
Chipping Sparrow	6	15
Mountain Bluebird	12	10
Bewick's Wren	4	20
Dusky Flycatcher	25	1
White-breasted Nuthatch	16	14
Violet-green Swallow	25	6
Bushtit	7	25
Green-tailed Towhee	25	8
Brown-headed Cowbird	9	25
Dark-eyed Junco	25	11
Hermit Thrush	25	12
Plain Titmouse	12	25
Rufous-sided Towhee	16	25
Brewer's Sparrow	25	16
Northern Flicker	25	17
Scrub Jay	19	25
Blue-gray Gnatcatcher	19	25
Fox Sparrow	25	19
Twenty-one additional rare species (index <0.1)[a]		

[a] The remaining species in common were rare in both zones: American Kestrel, Golden Eagle, Red-tailed Hawk, Broad-tailed Hummingbird, Downy and Hairy woodpeckers, Red-breasted Sapsucker, Mountain Quail, Common Raven, Mourning Dove, Say's Phoebe, Canyon Wren, Western Wood-Pewee, Tree Swallow, American Robin, Townsend's Solitaire, Solitary Vireo, Yellow-rumped Warbler, Western Tanager, Black-headed Grosbeak, Horned Lark.

years. Continued monitoring should determine if these species are undergoing directional changes in abundance.

For species with relatively high abundances (i.e., >0.1), the direction of change in abundance across years was the same for both zones, with the Mountain Chickadee and White-breasted Nuthatch declining, and the Gray Flycatcher and Rock Wren increasing. The Pygmy Nuthatch also declined in the bristlecone–limber pine zone, indicating that resource conditions for nuthatches were also declining across years. The Dusky Flycatcher declined in the bristlecone–limber pine zone, indicating that conditions there were differentially influencing the two *Empidonax* flycatchers (see below).

Declines in both zones included residents (i.e., Mountain Chickadee, Rufous-sided Towhee, Scrub Jay, nuthatches) and migrants (i.e., gnatcatcher, Dusky Flycatcher, thrush). The only migrant that increased was the Gray Flycatcher. The contrasting change in abundances of the *Empidonax* warrants further study.

Johnson and Cicero (1986) considered the Virginia's Warbler (*Vermivora virginiae*) fairly common but local in distribution in mountain mahogany–pinyon woodland in the White Mountains. We did not record this species during our counts and made only two sightings of it at other times (unpublished data). Thus, it appears that this species has undergone a substantial decline in abundance.

Reasons for these various changes in abundance are speculative but might involve the drought that began in California in 1986 and continued through our study. Snowpack and rainfall have been about 50% of normal each year throughout the drought (unpublished data; see also Morrison and Raphael [1993]). During our study no major cone crops were [illegible], and flowering and subsequent seed production in shrubs and annual plants has been poor (Hall et al. 1991, Hall 1992). Conditions on the wintering grounds might also have been responsible for changes in abundance of migrant species (e.g., Terborgh 1989). If future monitoring reveals continued changes in abundance of these bird species, then studies of their population biology should be initiated.

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REVISION OF THE GENERA OF PLATYPODIDAE (COLEOPTERA)

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ABSTRACT.— A search for characters to make the generic classification of Platypodidae more nearly objective resulted in the discovery of new anatomical features that appear to reflect patterns in phylogeny for this family. The Platypodidae are members of the Curculionoidea and are very closely allied to Scolytidae. Three subfamilies of Platypodidae are recognized: (1) Coptonotinae, containing Coptonotini (*Coptonotus* Chapuis, *Protohylastes* Wood, *Scolytotarsus* Schedl), Mecopelmini (*Mecopelmus* Blackman, *Protoplatypus* Wood), and Schedlarini (*Schedlarius* Wood [=*Chapuisia* Dugès]); (2) Tesserocerinae, containing Diapodini (*Diapus* Chapuis, *Genyocerus* Motschulsky [=*Diacavus* Schedl]) and Tesserocerini (*Platytarsulus* Schedl, *Notoplatypus* Lea, *Tesserocranulus* Schedl, *Tesserocerus* Saunders [=*Damicerus* Spinola, *Tesseroplatypus* Schedl, *Tesserocephalus* Schedl], *Spathidicerus* Chapuis, *Periommatus* Chapuis [=*Asetus* Nunberg, *Setanus* Nunberg], *Chaetastus* Nunberg [=*Symmerus* Chapuis], *Cenocephalus* Chapuis, and *Mitosoma* Chapuis [=*Platypicerus* Nunberg, *Coccephalonus* Schedl]); and (3) Platypodinae, containing Platypodini (*Platypus* Herbst [=*Cylindra* Illiger, *Stenoplatypus* Strohmeyer, *Platypinus* Schedl, *Austroplatypus* Browne], *Treptoplatypus* Schedl, *Crossotarsus* Chapuis, *Trachyostus* Schedl, *Neotrachyostus* Browne, *Platyscapulus* Schedl [=*Platyscapus* Schedl, *Costaroplatus* Nunberg], *Baiocis* Browne, *Cylindropalpus* Strohmeyer, *Triozastus* Schedl, *Mesoplatypus* Strohmeyer, *Doliopygus* Schedl [=*Scutopygus* Nunberg, *Pygodolius* Nunberg, *Mixopygus* Nunberg, *Mesopygus* Nunberg], and 11 genera named as new to science derived from the genus *Platypus* of Schedl 1972. The following are new genera and their type-species: *Peroplatypus* (for *Platypus truncatipennis* Schedl), *Dinoplatypus* (for *Platypus cupulatus* Chapuis), *Myoplatypus* (for *Bostrichus* or *Platypus flavicornis* Fabricius), *Oxoplatypus* (for *Scolytus* or *Platypus quadridentatus* Olivier), *Platyphysus* (for *Platypus obtusus* Chapuis), *Megaplatypus* (for *Platypus dentatus* Dalman), *Euplatypus* (for *Bostrichus* or *Platypus parallelus* Fabricius), *Epiplatypus* (for *Platypus desceptor* Wood), and *Teloplatypus* (for *Platypus concinnus* Blandford). The archaic "sektionen" used by Schedl in his 1972 classification of this family are eliminated. A key for the identification of genera, a discussion of characters, and remarks on phylogeny are included.

Key words. Platypodidae, Coleoptera, Platypus, *revision, taxonomy.*

During prepartion of the recent world catalog that included the family Platypodidae (Wood & Bright c1992), it was learned with considerable surprise that a systematic review of genera for this family did not exist. This contribution is written in an attempt to at least partially remedy that situation.

The group had its origin in systematics literature when Fabricius (1792:364) named *Bostrichus cylindrus* from Germany and assigned it to the non-Linnaean Xylophaga in the family Bostrichidae. A year later Herbst (1793:128) recognized the uniqueness of this species and erected the genus *Platypus* for it. *Platypus* was transferred by Latreille (1807:277) to his newly erected subfamily Scolytarii (currently Scolytidae) of his family Curculionites. Shuckard (1840 [reprinted 1861:64]) established the family Platypodidae for it. The group has received a tribe, subfamily, or family designation in virtually all treatments of the group since 1840. The family now contains slightly over 1400 species, almost all of which are tropical in distribution.

By 1861 approximately 17 species had been assigned to Platypodidae in *Platypus*, *Tesserocerus*, and *Genyocerus*. Chapuis (1865) added seven genera (*Cenocephalus*, *Crossotarsus*, *Diapus*, *Mitosoma*, *Periommatus*, *Spathidicerus*, *Symmerus* [=*Chaetastus*]) and about 220 species to the family in his classical Monographie des Platypides. This monograph (Chapuis 1865:22–23) contained the first key to genera used in the family. It was based largely upon mouthparts, eyes, and features of the prothorax. Species in the larger genera were divided into several archaic, non-Linnaean species-groups that were perpetuated by Strohmeyer (1912, 1914b), Schedl (1939–1972), and, to a lesser extent, by other authors.

Strohmeyer (1912) broadened the family to include the subfamily Chapuisiinae for *Chapuisia* Dugès (=*Schedlarius*), but he later placed it in a separate family, Coptonotidae

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Strohmeyer 1914a), a change followed only by Schedl (1939). Strohmeyer (1914b:18) divided the 323 known species of Platypodidae into two subfamilies based on the divided (Tesserocerinae) or undivided (Platypodinae) maxilla. The Tesserocerinae he then divided into tribes Tesserocerariae (*Tesserocerus*, *Periommatus*, *Spathidicerus*), Symmerariae (*Symmerus*), Cenocephalariae (*Cenocephalus*, *Mitosoma*), and Diapodariae (*Diapus*) based on procoxal, occular, and funicular characters. The Platypodinae were divided into tribes Platypodariae (*Platypus*, *Cylindropalpus*, *Notoplatypus*) and Crossotarsariae (*Crossotarsus*, *Stenoplatypus*, *Mesoplatypus*) based on characters of abdominal sternum 8. Strohmeyer perpetuated and expanded the non-Linnaean species-groups of Chapuis in his classification of the larger genera.

Schedl (1939) proposed a superfamily Scolytoidea in which he placed the families Scolytidae, Coptonotidae (for *Coptonotus*, *Scolytotarsus*, *Chapuisia*), Platytarsulidae (for *Platytarsulus*, *Notoplatypus*), and Platypodidae, with no subfamilies indicated, containing tribes Platypodini, Tesserocerini, Cenocephalini, Crossotarsini, Periomatini [*sic*], and Diaporini [*sic*]. Schedl's (1972) Monographie der Familie Platypodidae elevated the Crossotarsinae, Platypodinae, Periommatinae, and Diaporinae [*sic*] from tribal to subfamily rank, but reduced to subfamily rank the Platytarsulinae. The Tesserocerini and Cenocephalini were grouped within his Platypodinae. Schedl (1962) treated in his family Coptonotidae the genera *Coptonotus*, *Schedlarius* (=*Chapuisia*), and *Mecopelmus*. In his treatment of Platypodidae, Schedl (1939, 1972) perpetuated the use of the non-Linnaean species-groups of Chapuis with only minor modifications.

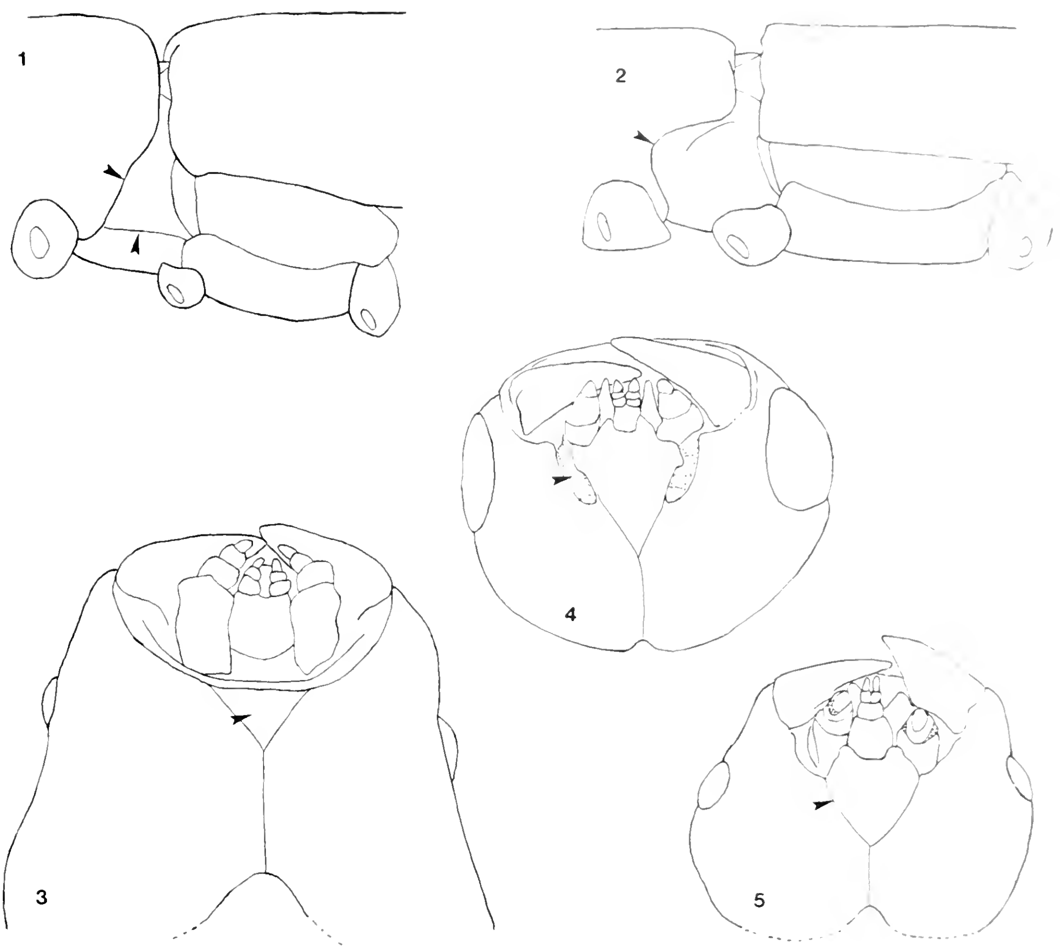
Wood (1973, 1986) included the Coptonotinae (Coptonotini, Mecopelmini, Schedlarini) in Platypodidae. Wood (c1992 *in* Wood & Bright) recognized the subfamilies Coptonotinae (tribes Coptonotini, Mecopelmini, Schedlarini), Tesserocerinae (tribes Diapodini, Tesserocerini), and Platypodinae (tribe Platypodini). A dendrogram that indicates possible phylogenetic relationships among these groups to one another and to Scolytidae appears in Wood (1982:13) except that the Tesserocerinae and Platypodinae are not divided.

While attempting to organize a reasonable arrangement of genera for the world catalog, I observed that some obviously related species had been grouped by Schedl (1972) in entirely different subfamilies, while other unrelated species had been clustered into the same genus, and I recognized that a serious generic revision has not been published on this taxon since the family was first recognized. The archaic classification then in use was unreasonable, unwieldy, and based as much on the whims of the taxonomist using it as on phylogeny or evolutionary relationships of the included taxa. This led to a search for characters that might be usable in a new classification.

REVIEW OF CHARACTERS

The Platypodidae are members of the superfamily Curculionoidea (Crowson 1955, 1968). They share many characters with other members of this group (Wood 1973, 1986). Within the Curculionoidea they are very closely allied to the Scolytidae with which they share the same broad ecological niche and many similar behavioral patterns. Together these two families share a conspicuous pregular sclerite (as defined by Hopkins 1909, 1911) that is clearly marked by sutures on both sides (Figs. 3–5) and is not similarly marked in any other family of Curculionoidea. Additional characters shared by these two families and those features that distinguish them from allied families are reviewed by Wood (1973, 1986). The feature most familiar to coleopterists and the one most widely employed in family keys for separating Platypodidae from Scolytidae is the length of tarsal segment 1 compared to segments 2–5. In Scolytidae segments 1, 2, and 3 are subequal in length, while in Platypodidae segment 1 is usually about as long as segments 2–5 combined (Wood 1986:11, fig. 9). However, in *Protoplatypus* (Mecopelmini) segments 1, 2, and 3 are subequal in length, while in *Mecopelmus* (Mecopelmini) segment 1 is as long as 2–5 combined. The remaining species of Coptonotinae are intermediate in their expression of this character (Schedl 1939:381, fig. 3).

The pregula sclerite in Coptonotinae (Fig. 3) is comparatively small as it is in Scolytidae; in Tesserocerinae (Fig. 4) and Platypodinae



Figs. 1–5. Platypodidae spp., males: 1, *Schedlarius mexicanus* (Chapuis), lateral aspect of thorax showing straight posterior margin of prothorax (upper arrow) and anapleural suture of mesothorax (lower arrow); 2, *Tesserocerus dewalquei* Chapuis, lateral aspect of thorax showing strongly procurved posterior margin of prothorax (arrow) and absence of a mesothoracic anapleural suture; 3, *Schedlarius mexicanus*, ventral aspect of head showing the small pregula (arrow) with its marginal sutures and transverse carina; 4, *Tesserocerus dewalquei*, ventral aspect of head showing the deep cleft (stippled area at arrow) between the large pregula and margin of the oral fossa, and 5, *Euplatypus parallelus* (Fabricius), ventral aspect of the head showing absence of the cleft (arrow).

(Fig. 5) it is much larger and very conspicuous. In Tesserocerinae there is a conspicuous cleft (Fig. 4, arrow) between the lateral margin of the pregula and the margin of the oral fossa (into which the maxilla moves). The depth of this cleft is usually equal to at least half the length of the pregula (Fig. 4). In Platypodinae this cleft is very shallow to nonexistent and is always equal in depth to less than one-fourth the length of the pregula (Fig. 5). The presence of this cleft is apparently correlated with the division of the maxilla into separate lacinia and galea lobes (Wood 1986:8, fig. 6); its absence appears to be correlated with the fusion of the lacinia and galea into one element. Due to the paucity of specimens available for study, *Platytarsulus* and *Notoplatypus* were assigned to Tesserocerinae on the basis of the presence of the cleft and were not dissected to determine the character of the maxilla.

In the Tesserocerinae the eye exhibits a departure from the usual subcircular, hemispherical shape. In *Platytarsulus*, *Spathidicerus*, and *Periommatus* the eye may be very large and reniform (Schedl 1939:384, fig. 4). In *Mecopelmus* (Coptonotinae) there is a slight modification in that direction (Blackman 1944:figs. 3–5).

Antennal characters appear to be significant in the early phyletic history of the Platypodidae. The antennal club is weakly marked by two strongly procurved sutures in *Coptonotus*; in the remainder of the family there is no evidence of sutures on the club. *Coptonotus* has the antennal funicle 7-segmented (Schedl 1939:380, fig. 2), a feature also shared with *Protohylastes* and *Scolytotarsus*. Because seven is the maximum number of segments in the funicle found in Curculionoidea (Crowson 1955, 1968), that number is assumed to exhibit the primitive character; any reduction from that number should represent specialization. In *Protoplatypus* and *Schedlarius* the funicle is 5-segmented, in *Mecopelmus* and *Notoplatypus* 3-segmented, in *Platytarsulus* 2-segmented, and in all other Tesserocerinae and in all Platypodinae it is 4-segmented (Schedl 1939:380, fig. 2). In *Coptonotus* and *Protohylastes* the antennal club is more slender and less strongly flattened than in other representatives of the family.

In Coptonotinae the posterior margin of the prothorax (as seen from a lateral aspect) is dorsoventrally straight to very weakly procurved; the mesepisternum is moderately large and almost flat (Fig. 1). In Tesserocerinae (Fig. 2) and Platypodinae the posterior margin of the prothorax is strongly procurved in the pleural area, the mesepisternum is inflated, or in specialized genera it may be impressed and variously carinate.

In all Coptonotinae and in Diapodini, *Tesserocerus*, and *Tesserocranulus* of the Tesserocerinae, the mesotergum is normal, that is, transversely flat or weakly, transversely convex. In all other Tesserocerinae and all Platypodinae it is armed by a conspicuous, strongly elevated, median carina. The presence of this carina represents an obvious specialization. In Scolytidae and Coptonotinae the mesothoracic anapleural (pleurosternal) suture is consistently present. This anapleural suture is largely (Tesserocerinae) or entirely (Platypodinae) eliminated in the higher Platypodidae.

Characters that might be used to indicate phylogenetic trends in Platypodinae are limited in number. A feature, apparently used here for the first time, is the presence of a groove or impression on the posterior portions of the metasternum and metepisternum for the reception of the metafemur. In the African genera *Cylindropalpus*, *Triozastus*, *Mesoplatypus*, and *Doliopygus*, the anterior margin of this impression is continuously carinate (or nearly so). In more than half (mostly American species) of what has previously been designated as *Platypus*, the anterior margin of this impression is marked by a series of minute spines, and in the remaining half of *Platypus* (mostly African and Indo-Australian species) the impression is weak to absent and spines are absent. Except for females of a few American species, this character appears to be a reliable indicator of relationship.

The visible abdominal sterna in Platypodidae exhibit rather limited, but remarkable, variation. The primitive structure appears to be five horizontal, unarmed segments that rise little, if any, to meet the apex of the elytral declivity. As the male declivity shortens (or atrophies) in some groups, the abdomen ascends gradually to abruptly to accommodate the change. In Diapodini (*Diapus*, *Genyocerus*) this ascent is almost entirely accomplished by visible sternum 5 as it becomes vertical and moderately to remarkably concave (This enables males of these genera forcefully to expel frass from the entrance hole 2 m or more from the host tree). In *Mesoplatypus* and *Doliopygus* a pronounced transverse carina occurs on visible sternum 2 (Schedl 1972:149, fig. 39); this enables sterna 3–5 (at least in *Doliopygus*) to become vertical and concave and to function much as does sternum 5 in the Diapodini. Less remarkable and less extensive variations occur on sterna 3, 4, or 5 where a transverse pair of moderate to elaborate spines (Wood 1966:47 [fig. 6], 67 [figs. 22–24]) arm one of these segments (sternum 3 in *Myoplatypus*, sternum 4 in *Oxyplatypus*, sternum 5 in *Platyscapulus*).

The protibia is somewhat uniform in the family except in primitive genera. It characteristically has a terminal mucro and is armed on the posterior (or lateral) face by one or more transversely carinate, coarse rugae. In female *Crossotarsus*, *Trachyostus*, and *Neotrachyostus*, and in at least two species of American *Megaplatypus*, these rugae are broken up and reorganized into numerous, confused granules. The socketed denticles (derived from setae) found in most Scolytidae (Wood 1986:11, fig. 10) are unknown in Platypodidae. The tibial denticles of Platypodidae are true spines that function in gripping tunnel walls. The simplest form appears to be that of *Protohylastes* (Wood 1973:86, fig. 25). Other Coptonotinae may have one lateral spine or carinate ruga; higher genera have two to nine rugae (Wood 1973:86, figs. 25–33, Schedl 1939:379, fig. 1). The rugae are not always consistent in position and form in the higher genera and must be used in classification with caution.

Tarsal segment 3 is slender and cylindrical in almost all Platypodidae (Wood 1986:11, fig. 9). In the Coptonotinae genera *Coptonotus*, *Protohylastes*, *Scolytotarsus*, and *Schedlarius* segment 3 (Schedl 1939:381, fig. 3) is broad and strongly bilobed as in primitive Curculionoidea.

The spines arming the male elytral declivity are truly remarkable and almost endlessly diverse within the Platypodidae. However, as groups are segregated on the basis of other characters, the constancy and usefulness of these spines and patterns of spines become apparent. Greater knowledge of Platypodidae pairing and mating behavior would probably increase our understanding of the significance of size and position of these spines.

It is generally understood that all Platypodidae (except *Protoplatypus*) are monogynous, and in all species the male initiates the formation of a new parental gallery system. The female, consequently, assumes the primary responsibility for the identification and acceptance of a male. Presumably, for this reason, the male posterior extremities exhibit remarkable characters, while the females exhibit few, often very subtle, distinguishing features. Perhaps the most remarkable female features are the dehiscent mandibular appendages of the Diapodini (Roberts 1993) that are used briefly for tactile communication with the male at pairing and/or mating and are then discarded. A few other females that possess remarkable frontal characters apparently use those features in caring for the eggs or larvae (Wood 1986:4, fig. 2). This is an area where very little factual information is available. The mycetangia pores on the pronotum of many female (and a few male) Platypodidae appear to follow distinguishable patterns in some groups. These patterns appear more constant and less diverse than previous usage might suggest.

The three genera of Coptonotinae studied in the field by me have habits more nearly like Scolytidae than like other Platypodidae. In *Schedlarius* (Wood 1957), parent adults make long egg tunnels in the xylem; egg niches are randomly formed on all sides of the tunnel into which the eggs are placed, one in each niche, and packed in frass. The larvae form long, independent, winding tunnels in the xylem. Although fungal decay in the vicinity of boring activity of both adults and larvae was obvious, there was no ambrosial mycelium growth on the walls of adult or larval mines. Adult *Mecopelmus* form a simple cave tunnel, about 1 cm in diameter and 1–2 mm deep, at and slightly below the cambium region of their host. In the frass of this chamber the female deposits a cluster of one or two dozen eggs. The first- and second-instar larvae feed on this frass and then bore individual mines in the cambium region as they radiate out from the central chamber. There was no evidence of mycelial growth in the mines at 20X magnification. *Protoplatypus* parent adults formed radiate tunnels (with 3–5 egg galleries in each, similar to those of *Pityophthorus*) in the cambium of their host, complete with nuptial chamber, egg galleries, egg niches, and individual larval mines. Mycelial growth was not evident at 20X magnification. All other observed Platypodidae (Tesserocerinae and Platypodinae) are xylomycetophagous.

PHYLOGENY

The Platypodidae and Scolytidae are very closely related to one another, so much so that four of the six genera of Coptonotinae could be assigned to either family without serious conflict. The most closely allied groups within the Scolytidae to the Coptonotinae, however, appear to be in or near the Carphodicticini or possibly the Dryocoetini of the Scolytidae, rather than the superficially similar tribes in what has been regarded as the more primitive Hylesininae. The Platypodidae appear to be the first of eight phyletic lines within the Platypodidae-Scolytidae group to adopt the xylomycetophagous habit. This shift in adaptive specialization had a profound impact on form and function within the Platypodidae that separated them rather sharply from the Scolytidae.

Few detailed anatomical studies have been based on members of the Platypodidae, and, for the most part, those that have been made were based on the accessible, more specialized representatives.

It is almost universally agreed that the Platypodidae-Scolytidae are members of the Curculionoidea (Crowson 1955, 1968:154–166, Wood 1973, 1986). Exactly where these families fit within the Curculionoidea has been the subject of much discussion and disagreement. Their traditional placement within (Crowson 1955, 1968, as subfamilies) or adjacent (as families) to Curculionidae is questioned by me (Wood 1973, 1986). Their placement among the higher Curculionoidea is substantiated by the presence of only one median, gular suture (Wood 1986:6, 8); however, the very short length of this suture in Platypodidae is a departure from most other Curculionoidea and could have significance. The comparative positions of the mandibular condyles, including conspicuous reduction of the hypostomal area, also sets the Platypodidae-Scolytidae apart from other Curculionoidea, particularly the Cossoninae (Curculionidae) to which they are supposed to be closely related (Wood 1986:10, fig. 8). The truly unique character of the Platypodidae-Scolytidae is the conspicuous pregular sclerite that is clearly marked on both sides by sutures (Figs. 3–5), a feature that is shared by no other family (Wood 1986:6–8). In Anthribidae and Nemonychidae the lacinia and galea form separate elements on the maxilla. Among those Curculionoidea having only one gular suture, the maxilla is similarly divided only in some Attelabidae, some Rhynchitidae, and the subfamily Tesserocerinae of the Platypodidae (Wood 1986:8, fig. 6). No member of the Curculionidae shares this character. The loss of the mesothoracic anapleural suture in Tesserocerinae (Fig. 2) and Platypodinae appears to have occurred entirely within the Platypodidae because it is present in all Coptonotinae (Fig. 1) and in all Scolytidae. Browne (1972) reported urogomphi-like structures in larvae of two species of African Platypodidae; if correct, this would be the only known occurrence of these structures in Curculionoidea. The true homology of a labrum-like structure in *Chaetastus* (Wood 1986:4, fig. 2) and other female Tesserocerini has not been clarified. Evolution within the Curculionoidea is obviously much more complex than published simplistic explanations acknowledge. Obviously many unanswered questions remain that must be answered before reasonable explanations are found.

To summarize the above, it appears that the Platypodidae-Scolytidae represent a distinct phyletic line of Curculionoidea having one gular suture and that this line is independent from the Brenthidae-Rhynchitidae-Curculionidae line of specialization.

Phyletic trends within the Platypodidae are somewhat unclear. The six genera of Coptonotinae (represented by nine rare species scattered on four tropical contenents and New Guinea) appear to represent relict remains of a once much larger group. All lack the median mesonotal carina once thought to characterize all representatives of this family, and all have the anapleural suture on the mesopleuron. Four of these genera (*Coptonotus, Protohylastes, Scolytotarsus, Schedlarius*) have tarsal segment 3 broad and bilobed. None of the six has the antennal funicle 4-segmented as it is in all but two genera of the remainder of the family. However, none of these six genera has the maxilla divided into separate lacinia and galea. The three genera for which habits are known all lack the xylomycetophagous habit. Of these six genera, *Coptonotus* and *Protohylastes* are closely allied to one another and approach the Scolytidae more closely in structural detail than do the other four. *Schedlarius* appears to be the most closely allied to other Platypodidae of these six. *Protoplatypus* and *Mecopelmus* are allied to one another but appear to represent an independent evolutionary experiment with no close alliance to any other group.

The Tesserocerinae are characterized by the division of the maxilla into separate lacinia and galea elements (Wood 1986:8, fig. 6) and by the accompanying cleft between the pregula and margin of the oral fossa (Fig. 4). This feature suggests a relationship to the most primitive Curculionoidea families. Within the subfamily, the Diapodini (*Diapus, Genyocerus*), *Tesserocerus*, and *Tesserocranulus* lack a median carina on the mesotergum. The Diapodini also have the procoxae widely separated, a primitive feature, but the mycetangia pores on the pronotum and the highly specialized abdominal sternum 5 represent extreme specialization. *Platytarsulus* (2-segmented) and *Notoplatypus* (3-segmented) have a reduced number of segments in the antennal funicle. These six genera have the protibia more slender and with fewer transverse, carinate rugae on the posterior (or lateral) face. They probably represent the more primitive element of the family after family characters were firmly fixed.

The (a) Diapodini, *Platytarsulus*, and *Notoplatypus* are exclusively Indo-Australian in distribution (except for one species of *Diapus* recently introduced through modern commerce into Africa) and each is without a close living relative; (b) *Spathidicerus* (Indo-Australian) and *Periommatus* (African) are obviously derived from a common ancestor and are closely related to one another; (c) *Tesserocerus* and *Tesserocranulus* (both tropical American) are also allied to one another; (d) *Chaetastus* (African), *Mitosoma* (Madagascaran), and *Cenocephalus* (tropical American) are also allied to one another, but are quite distinct from other Tesserocerini. It appears that groups a, b, and c have evolved entirely since the early Tertiary separation of Africa and South America. Only group d exhibits a phyletic imprint of pre-Tertiary development. It is concluded, therefore, that the evolution of the Tesserocerinae has been rapid and that pre-Tertiary representatives of this subfamily must have been radically different from modern taxa.

In the Platypodinae (Platypodini) four lines of development are seen: (a) *Platypus* (largely African to Indo-Australian), *Treptoplatypus* (Indo-Australian, Oriental, NW North American), *Peroplatypus* (Indo-Australian), *Dinoplatypus* (Indo-Australian); (b) *Crossotarsus* (Indo-Australian), *Trachyostus* (African), *Neotrachyostus* (tropical American); (c) *Platyscapulus* (tropical American), *Myoplatypus* (American), *Oxoplatypus* (American), *Platyphysus* (tropical American), *Megaplatypus* (tropical American), *Euplatypus* (mostly American, some African, Madagascaran), *Baiocis* (Indo-Malayan), *Epiplatypus* (tropical American), *Teloplatypus* (tropical American); (d) *Cylindropalpus* (mostly African, 1 Madagascaran), *Triozastus* (African), *Mesoplatypus* (African), *Doliopygus* (African). Group a occurs primarily in the Indo-Australian area, with slight, recent invasion of Africa, and one species of uncertain affinity in tropical America. Group b appears to have occupied the Indo-Australian, African, and South American areas before the separation of Africa and South America and suggests a pre-Tertiary origin. Group c is primarily American except for *Baiocis* that is of uncertain affinity, and *Euplatypus* that appears to have had early interaction with Madagascar and a later exchange from Madagascar to Africa [The modern circumtropical extension through commerce of *parallelus* from America is ignored]. Group d is exclusively African except for one species that reached Madagascar from Africa rather recently. Based on these data, it appears that evolution of the Platypodinae has been rapid since the early Tertiary separation of Africa and South America and that pre-Tertiary taxa must have been structurally very different from modern species. Pre-Tertiary Platypodinae must have resembled the Coptonotinae much more than has previously been supposed and suggests an origin no earlier than that of flowering plants (Lower Cretaceous).

SYSTEMATIC SECTION

Because this represents the first real examination of generic classification in Platypodidae since the family was established, some radical departures from previous treatments are recommended. Foremost among these is the abandonment of the archaic practice of employing undefinable species-groups or infrageneric groups below the genus level and above the species rank. Schedl (1972) employed 62 of these groups in his treatment of the genus *Platypus*. This change made it necessary to retrieve a number of generic names that had previously been placed in synonymy and to name several others. Although this will cause some initial confusion, it should ultimately enhance communication on this family.

The treatment of genera following the key is brief except in the tribe Platypodini (subfamily Platypodinae) because of the significant changes introduced there. The treatment of the six genera of Coptonotinae is virtually unchanged from previous usage. The significant changes in Tesserocerinae include (1) the transfer of *Platytarsulus* and *Notoplatypus* into the subfamily from Platypodinae, and (2) the restoration of *Chaetastus*, *Cenocephalus*, and *Mitosoma* to full generic rank.

This study was based on my personal collection of over 100 species of Platypodidae and my examination of more than 400 other species. Because approximately half of the known species in the family were not seen by me, it is obvious that adjustments in the proposals made here will be needed in the future.

The monobasic genera *Crossotarsinulus* Schedl (1972:84–87) and *Spathicranuloides* Schedl (1972:71) are unknown to me and, consequently, were not included in this study.

Key to the Genera of Platypodidae

1. Posterior margin of prothorax (as seen from lateral aspect) straight to weakly procurved in pleural area (Fig. 1); mesepisternum moderately large, almost flat; mesotergum flat to broadly, transversely arched, without a conspicuous, acute, median carina, scutellum rising abruptly to elytral surface; pronotum never with mycetangia grooves or pores; pregula small, bearing a transverse carina; eyes sometimes large, elongate, flat; antennal scape slender, club-shaped; procoxae smaller, usually on middle third of prosternum length, tarsal segment 1 short (except elongate in *Mecopelmus*, *Schedlarius*); anapleural suture on mesothorax present (Fig. 1); xylophagous or phloeophagous; Coptonotinae 2

— Posterior margin of prothorax strongly procurved in pleural area (Fig. 2); mesepisternum large, usually inflated (concave in some Tesserocerinae), pronotum often with conspicuous grooves or pores extending into mycetangia; mesotergum usually bearing a conspicuous median carina (absent in four genera), scutellum, if present, rising gradually (usually carinate and apically pointed); procoxae enlarged, occupying posterior half of segment, pregula moderately to very large, usually flat (never with a transverse carina); antennal scape variously modified; eyes usually rounded, hemispherical; tarsal segment 1 always elongate, usually longer than segments 2–5 combined; anapleural suture on mesothorax largely or entirely absent (Fig. 2); xylomycetophagous......7

2(1). Antennal funicle 7-segmented, club slender, small; profemur more slender, at least 2.6 times as long as wide; protibia more slender and almost as long as femur; pregula with a higher median carina arising from a low transverse carina and terminating cephalad in a small, blunt spine; species larger than 3.5 mm, stouter, darker in color; (Coptonotini) 3

— Antennal funicle 3–5-segmented, club larger, broader, more strongly flattened; profemur stouter, less than 2.0 times as long as wide (except slender in *Schedlarius*); protibia stouter, conspicuously shorter than femur; pregula without a median carina or spine; either pale species smaller than 2.0 mm or very slender..5

3(2). Eye very large, flat, subreniform; antennal club inconspicuously marked by two strongly procurved, subangulate sutures, these weakly indicated by grooves and setae; color almost black; tropical America; 3.2 or 9.0 mm ....***Coptonotus* Chapuis**

— Eye short, subcircular to oval in outline, less than 1.5 times as long as wide; antennal club unmarked by sutures; Africa or Australia.. 4

4(3). Eye oval, about 1.5 times as long as wide; protibia very slender, its apex armed by a small median spine, a minor spine on each side near apex; body and pronotum hylesinine in form; Australia; 9.8 mm..***Protohylastes* Wood**

— Eye, subcircular, hemispherical; protibia distorted by a large spine near its middle; body and pronotum platypodine; Africa and Australia; 4.5–4.9 mm ....***Scolytotarsus* Schedl**

5(2). Protibia small, with a terminal mucro and with or without one spine on lateral margin; tarsal segment 3 narrow, cylindrical; elytra simple, declivity convex, unarmed; pale species, body less than 2.0 mm; (Mecopelmini) 6

— Protibia larger, subapically armed on lateral face immediately above tarsal insertion by one transverse, coarse, costate ruga; tarsal segment 3 very broad, deeply bilobed; antennal funicle 5-segmented; elytral declivity obliquely subtruncate, its margin costate on lower half, armed above by a row of several small spines, its face on interstriae ornamented by numerous small, white scales; Mexico to Panama; xylophagous in *Bursera* spp.; 4.0–7.0 mm; (Schedlarini)........ ....***Schedlarius* Wood**

6(5). Antennal funicle 5-segmented, posterior face of club glabrous; eye smaller, finely faceted; abdomen horizontal, costal margin of elytra horizontal or descending to apex; tarsal segment 1 short, subequal in length to 2 or 3; adults polygynous, parental tunnels radiate, in cambium, first-instar larvae form individual tunnels in cambium; New Guinea; 1.2–1.5 mm........................***Protoplatypus* Wood**

— Antennal funicle 3-segmented, club pubescent on both faces; eye larger, coarsely faceted, abdomen distinctly ascending behind, costal margin of elytra ascending on apical one-fifth; tarsal segment 1 as long as 2–5 combined; adults monogynous, parental chamber a simple cave, third-instar larvae form independent tunnels radiating from central chamber in *Serjania* spp., Panama, 1.4–1.6 mm .... ***Mecopelmus*** **Blackman**

7(1). Maxilla with mesal element clearly divided into separate lacinia and galea; pregula separated on each side from margin of oral fossa by a deep cleft (into which maxilla moves) equal to at least one-half pregula length, visible pregula caudad from cleft comparatively small; Tesserocerinae 8

— Maxilla with lacinia and galea combined into one mesal element; pregula large to very large, cleft between pregula and oral fossa nonexistent to shallow, equal to less than one-fourth pregula length; Platypodidae, Platypodini 18

8(7). Procoxae widely separated, each coxa very large, longer than tibia; mesonotum flat or evenly, transversely arched, without a conspicuous median carina; scutellum rather large, broad; male abdominal sternum 5 subvertical, usually concavely excavated; (Diapodini) 9

— Procoxae contiguous, each coxa shorter than tibia; mesonotum with a conspicuous, acute, median carina (except flat, without a carina, in *Tesserocerus*, *Tesserocranulus*); scutellum small, slender, pointed; (Tesserocerini) 10

9(8). Anterior face of antennal club with a small area or line smooth, shining, often weakly elevated; base of female pronotum (occasionally also male) with a band of many mycetangia pores or grooves, scutellum smaller, narrower, often depressed, frons more sparsely pubescent in both sexes, newly emerged female usually with dehiscent mandibular appendages; Africa to Taiwan and Australia; 1.8–5.0 mm .... ***Diapus*** **Chapuis**

— Antennal club uniformly pubescent to base, base of pronotum ornamented in median area by few coarse mycetangia pores, never with grooves; scutellum larger, broader, higher; female frons usually ornamented by tufts of very long setae; female dehiscent mandibular appendages usually absent, India to Philippines and New Guinea, 1.7–4.0 mm .... ***Genyocerus*** **Motschulsky**

10(8). Antennal funicle 2–3-segmented, club with large procurved, glabrous, basal area extending at least one-half length of club, margins and apical area minutely, closely pubescent; protibiae armed by lateral spine at tarsal insertion and one additional subapical spine or ruga; elytral declivity gradual, weakly armed; pronotum and elytra reticulate 11

— Antennal funicle 4-segmented; club either pubescent to base or glabrous area much smaller (basal one-fourth); protibia usually more elaborately armed 12

11(10). Antennal funicle 2-segmented; eye elongate, reniform, at least 2.0 times as long as wide; protibia with one transverse ruga above lateral spine; Borneo to Malaya; 1.5 mm .... ***Platytarsulus*** **Schedl**

— Antennal funicle 3-segmented; eye subcircular, as wide as long, entire; protibia with a small tubercle on margin above lateral spine; Australia, *Eucalyptus* spp.; 5.5–[illegible] mm .... ***Notoplatypus*** **Lea**

12(10). Eye elongate, 1.5 or more times longer than wide, almost flat; mesepisternum flattened to concavely excavated, its upper (and sometimes anterior) margin armed by a fine conspicuous carina (carina absent in some *Spathidicerus*); anterior margin of mesocoxal cavity acutely carinate, carina curving cephalad and ending in margin of mesepisternum; pronotum more slender, 1.4–4.0 times as long as wide; precoxal piece on prosternum acutely pointed 13

— Eye subcircular, little if any longer than wide, hemispherical; mesepisternum convex, never armed by a carina, anterior margin of mesocoxal cavity never continued cephalad as a carina; pronotum stouter, 1.0–1.3 times as long as wide; precoxal piece on prosternum obtusely pointed; pronotum and elytra rarely reticulate 16

13(12). Mesonotum almost flat, never marked by a median carina; eye shorter, oval to subtriangular in outline, 1.2–2.0 times as long as wide, anterior margin entire; Neotropical species 14

— Mesonotum conspicuously armed by a strongly elevated, acute, median carina; eye very large, reniform, its anterior margin broadly emarginate, often two or more times longer than wide; African and Indo-Australian species 15

14(13). Small, exceedingly slender species, body at least 8.0 times as long as wide; lateral margin of pronotum acute; lateral margin of posterior one-third of prosternum with a deep, longitudinal, pleural groove between notal and sternal margins; female scape remarkably flattened and broadly expanded mesad, dorsad, and caudad, scape inserted one-third scape length from base; Costa Rica to Cayenne; 4.0–4.2 mm .... ***Tesserocranulus*** **Schedl**

Larger [illegible] species, 3.0–4.5 times as long as wide; pronotum narrowly to subacutely rounded on lateral margins, prosternum never with lateral margin costate, without a narrow, pleural groove between these margins; female scape slender, with pedicel attached near its apex, a slender, elongate extension in a few species; Mexico to Argentina, 3.0–11.0 mm .... *Tesserocerus* **Saunders**

15(13). Mesepisternum flat and unarmed by a carina (larger species) or concavely excavated and its margin armed by a carina (smaller species); pronotal constriction (in which protibia moves) shallow, its posterior portion gradual, not extended ventrad, pleural impression mostly below pronotal margin; protibia armed by only two coarse, transverse rugae; Indonesia to New Guinea and Philippines; 4.0–12.0 mm .... *Spathidicerus* **Chapuis**

— Mesepisternum always concavely excavated, its margin armed by a carina; pronotal constriction much deeper, its posterior portion abrupt, with notum extending more ventrad; protibia armed by three coarse, transverse rugae; Africa; 2.2–5.0 mm .... *Periommatus* **Chapuis**

16(12). Posterior one-third of pronotum with a transverse band of numerous, small, closely placed mycetangia pores; anterior face of metatibia armed by only one transverse ruga; striae more distinctly impressed, punctures clearly visible; female frons impressed from eye to eye, central two-thirds of impressed area abruptly, deeply excavated on a circular area; elytral declivity convex, rather steep, spines short, rather inconspicuous; larger, stouter species; Africa; 3.9–7.0 mm .... *Chaetastus* **Nunberg**

— Pronotal punctures uniform throughout, mycetangia pores not discernible; anterior face of metatibia armed by three or more transverse rugae; striae weakly if at all impressed, punctures evident or not; female frons variously impressed from eye to eye, without an abrupt, deep, central excavation; smaller, more slender species 17

17(16). Male elytral declivity usually convex, very steep, usually not excavated, spines smaller, if evident; base of male declivity usually not armed by spines; Central and South America; 2.5–4.2 mm. .... *Cenocephalus* **Chapuis**

— Male elytral declivity usually obliquely truncate and variously excavated, spines much larger; base of male declivity usually armed by spines; Madagascar; 3.7–4.0 mm .... *Mitosoma* **Chapuis**

18(7). Metasternum and metepisternum near metacoxa usually weakly or not impressed for reception of femur, anterior margin of impressed area never continuously carinate or armed by a row of small spines (one coarse nodule present on metepisternum in male of some large *Crossotarsus*), surface of impressed area with at least some setae; protibia of male armed by about four or more coarse, transverse rugae, female either similar to male or sometimes mostly covered by small, confused granules and usually one or two weak rugae near tarsal insertion; if present on female pronotum, mycetangia pores numerous 19

— Metasternum and metepisternum near metacoxa impressed for reception of femur, anterior margin of impressed area either continuously carinate or armed by a series of small spines (absent in occasional females and in American allies of *Euplatypus longulus*), surface of impressed area glabrous; protibiae of males and females similarly armed by rugae; spines on one or more abdominal sterna (couplet 27) a common feature; mycetangia pores variable 25

19(18). Male and female protibiae similarly armed by rows of transverse rugae 20

— Male protibia armed by transverse rugae, female protibia largely granulate, with no more than one or two weak rugae near apex 23

20(19). Suture at apex of male elytral declivity entire, declivity variously convex, with or without armature of tubercles and spines; if present, female mycetangia pores on pronotum numerous; worldwide in most tropical and subtropical areas, only 1 species in America; 2.5–10.5 mm .... *Platypus* **Herbst**

— Male declivity abruptly truncate, its margin obtuse to very acutely costate on almost a complete circle, apex sometimes strongly, attenuately narrowed, declivital face usually concave; mycetangia pores variable 21

21(20). Elytral apex of male moderately to exceedingly attenuate, strongly narrowed to true base of declivity, dehiscence of suture sometimes small, obscure, basal margin of declivity usually more gradual, sometimes rounded; India and Australia to Japan and NW North America; 2.4–6.0 mm .... *Treptoplatypus* **Schedl**

— Male elytral declivity much more broadly truncate, declivital base almost as wide as base of elytra, basal margin abrupt, obtusely to very acutely margined 22

22(21). Male sutural apex of declivity usually entire, slightly dehiscent in one species; male elytra not distinctly constricted before declivity, costa at base of declivity obtuse to subaente, interstrial rows sometimes indicated on upper portion, at least a few setae present, declivital face largely dull in most species, shining in one; Malaya to New Guinea; 2.8–4.5 mm ....***Peroplatypus*** **Wood**

— Male sutural apex modestly to very strongly, very broadly emarginate; margin at base of male declivity moderately to strongly acute, face of declivity smooth, shining, glabrous, striae and interstriae never indicated, male declivity with a distinct constriction slightly anterior to declivital base; India and Japan to Australia and Micronesia; 2.8–5.5 mm ....***Dinoplatypus*** **Wood**

23(19). Male declivity very short to absent, usually subvertical, a row of spines usually arms base of declivity, venter of abdomen rising abruptly to meet elytra; male metepisternum of larger species often armed near posterior end by one rounded nodule; India and Australia to Taiwan and Hawaiian Islands; 3.6–10.5 mm ....***Crossotarsus*** **Chapuis**

— Male elytra strongly, more gradually declivous, venter of abdomen more nearly horizontal on segments 2–5; metepisternum never armed by a nodule 24

24(23). Ventrolateral margin of male elytral declivity evenly rounded, never serrate or dentate, its basal margin weakly armed, never dentate; male declivity usually convex, surface dull; female pronotum never with mycetangia pores; Africa; 4.8–9.5 mm ....***Trachyostus*** **Schedl**

— Ventrolateral margin of male declivity variously serrate, dentate, or emarginate, its basal margin variously carinate or armed by spines; male declivital surface subconcavely excavated; female pronotum with a pair of mycetangia pores near median line on basal half; S Mexico to Brazil; 5.0–7.5 mm ....***Neotrachyostus*** **Browne**

25(18). Anterior margin of impression on metasternum and metepisternum for reception of femur armed by a series of small, pointed spines (sometimes obscure or absent in female *Euplatypus*); American or Madagascar species, four from Africa....................26

— Anterior margin of impression on metasternum and metepisternum armed by a complete or interrupted costa, rarely reduced to one (somewhat pointed) subcostate spine; African species.................................34

26(25). Male visible abdominal sternum 3, 4, or 5 armed by a pair of widely (transversely) separated coarse spines 27

— Male abdominal sterna 3–5 never armed by spines..29

27(26). Visible male abdominal sternum 5 armed by a pair of widely separated spines, male elytral declivity shorter, steeper, its ventrolateral angles poorly developed and projecting little if any, male interstriae on posterior half of disc usually carinate, pronotum never with mycetangia pores in either sex, small species, 1.9–3.5 mm, Mexico to Argentina.... .... ***Platyscapulus*** **Schedl**

— Visible male abdominal sternum 3 or 4 armed by a pair of widely separated spines, male elytral declivity more gradual, ventrolateral angles more strongly produced, discal interstriae in male never carinate, pronotum on basal half often with a pair of mycetangia pores in female or in both sexes... . 28

28(27). Visible male sternum 3 armed by a pair of spines; male declivity often steeper, shorter, mycetangia pores on pronotum often present in female or in both sexes, SE USA to Venezuela; 2.0–5.5 mm ....***Myoplatypus*** **Wood**

— Visible male sternum 4 armed by a pair of spines; male pronotum without mycetangia pores, female with 1 pair of unusually large pores; *Quercus* spp., S USA to Chihuahua and Nyarit in Mexico; 3.5–4.5 mm ....***Oxoplatypus*** **Wood**

29(26). Male elytra rather strongly declivous on posterior one-third, declivity variously convex or obliquely impressed, with or without armature; venter of male abdomen rising only slightly to meet apex of elytra 30

— Male elytra descending little if any before apex, declivity short, subvertical, if evident venter of male abdomen rising more than one-half distance to meet apex . . 32

30(29). Venter of male abdomen horizontal to sternum 5, sternum 5 moderately to strongly inflated, its apical one-fourth ascending rather abruptly to meet apex of elytra, male elytral declivity strongly convex, steep, unarmed or with small denticles on interstriae 3, 7, 9, none on apical margin, mycetangia pores on pronotum never present in either sex, Costa Rica to Brazil, 2.3–4.0 mm .... ***Platyphysus*** **Wood**

— Venter of male abdomen rising almost one-half distance to meet apex of elytra, declivity descending moderately, often variously impressed and armed by spines . 31

31(29) Male declivity with ventrolateral angles usually formed and modestly produced, their apices never exceeding apical margin at suture, margin between ventrolateral angles frequently armed by one or more pairs of denticles or serrations, mycetangia pores on pronotum uncommon in female, rare in male, when present, consisting of one pair or paired small clusters. Mexico to Argentina; 2.5–10.0 mm......***Megaplatypus*** **Wood**

— Male declivity with ventrolateral angles more strongly produced, usually exceeding apical margin at suture, projecting process usually more slender and often with its apex bi- or tridently armed, never with serrations or denticles on apical margin between processes; pronotum often with one pair of mycetangia pores in female, less common in male; mostly Mexico to Argentina, a few in Africa and Madagascar, *parallelus* circumtropical; 2.3–7.0 mm...............***Euplatypus*** **Wood**

32(29) Male declivity not descending, unarmed; male abdominal sternum 5 concave; small, reticulate, very slender species, 5.0 or more times as long as wide, upper surfaces usually reticulate; numerous mycetangia pores on pronotum, if present; sexual dimorphism obscure; Australia to Malaya; 1.7–2.4 mm..... ....***Baiocis*** **Browne**

— Less slender species; sexual dimorphism conspicuous, male declivity always with small spines; when present, mycetangia pores limited to one pair; American species....33

33(32) Male declivity with two pairs of serrations on ventrolateral margin, these serrations usually connected by a carina, median pair (often both) on apical margin; one pair of mycetangia pores on pronotum often present; Costa Rica to Brazil; 2.8–4.5 mm........... ....***Epiplatypus*** **Wood**

— Male declivity with only one pair of serrations on ventrolateral margin, a carina extending dorsad from this spine to a spine on interstriae 3 at base of declivity, basal margin at apex of disc usually armed by small spines on interstriae 1, 3, 5; mycetangia pores on pronotum never present; S Mexico to Argentina; 2.2–4.2 mm................. ....***Teloplatypus*** **Wood**

34(25) Male abdomen with sternum 2 normal, sterna gradually ascending from 1–5, unarmed; declivity descending slightly to moderately; female frons often variously concave 35

— Male abdomen with sternum 2 abnormally long, armed or abruptly angled on 2, ascending from 3–5; female frons often densely pubescent 36

35(34) Male abdomen with sterna 1–5 transversely convex, with normal rotation; elytral declivity convex, descending about one half distance to meet ascending abdomen; declivital tubercles small, inconspicuous; female frons broadly and shallowly to strongly concave; Africa, Madagascar; 2.5–5.5 mm........ ....*Cylindropalpus* Strohmeyer

— Male abdomen broadly concave, both transversely and longitudinally, from base of sternum 1 to apex of 5, impressed area often elaborately pubescent; declivity descending very slightly, its margin armed by spines, interstriae 1 near its apex diverging laterad moderately and descending slightly before its apex; female frons with a pair of small to moderately large concavities in lateral areas between base of mandibles and antennal insertions; Africa; 3.0–4.0 mm...................... ....***Triozastus*** **Schedl**

36(34) Male abdominal sternum 2 often armed by a pair of coarse, blunt spines, 3–5 ascending and sometimes armed on one or more of these segments by small spines; male declivity descending moderately, armature rather inconspicuous; female frons concavely impressed; Africa; 3.5–4.5 mm.................. ....***Mesoplatypus*** **Strohmeyer**

— Male abdominal sternum 2 transversely carinate, carina moderately to extremely, strongly elevated and either continuous or interrupted near median line; declivity usually armed on its basal margin by dorsoventrally flattened costae, these costae interrupted at strial intervals, declivity below these spines weak to nonexistent; female frons variously sculptured, often elaborately ornamented by setae; Africa; 2.5–7.0 mm ....***Doliopygus*** **Schedl**

COPTONOTINAE

The classification of Coptonotinae remains as presented in Wood *in* Wood & Bright (c1992), containing the following: Coptonotini (*Coptonotus* Chapuis, 2 Neotropical species; *Protohylastes* Wood, 2 Australian species; *Scolytotarsus* Schedl, 1 African and 1 Australian species); Mecopelmini (*Mecopelmus* Blackman, 1 species from Panama; *Protoplatypus* Wood, 1 species from New Guinea); and Schedlarini (*Schedlarius* Wood, 1 species from Mexico). *Mecopelmus zeteki* Blackman is known only from specimens collected within 2 km of the Panama Canal. It is quite probable that this species was introduced from another part of the world, possibly New Guinea where the only known relative occurs.

TESSEROCERINAE

The Tesserocerinae are divided into two tribes as presented in Wood *in* Wood & Bright (c1992): Diapodini (*Diapus* Chapuis, 39 species from India to Australia; *Genyocerus* Motschulsky [=*Diacavus* Schedl], 24 species from India and Sri Lanka to Philippines and New Guinea); and Tesserocerini.

A divided maxilla into separate lacinia and galea lobes occurs in the primitive Curculionoidea (Anthribidae, Nemonychidae) having two gular sutures (Crowson 1955, 1968, Wood 1986). Among the higher Curculionoidea, those with only one gular suture, divided lacinia and galea lobes occur only in parts of Attelabidae, Rhynchitidae, and Platypodidae (Tesserocerinae; Wood 1986:8, fig. 8). In all three of these families the taxon containing all species with separate lacinia and galea is given subfamily status. Strohmeyer (1912, 1914b) appreciated this fact and recognized the subfamily Tesserocerinae. Schedl (1972) was not a student of evolution and did not acknowledge the existence of this character in Platypodidae.

To the Tesserocerini of Strohmeyer (1912, 1914b) two genera are added here, *Platytarsulus* Schedl and *Notoplatypus* Lea, on the basis of the deep cleft between the pregula and the margin of the oral fossa (specimens for dissection of the maxilla were not available). The Tesserocerini now contain (Wood *in* Wood & Bright c1992) the following: *Platytarsulus* Schedl (8 species from Malaya and Borneo); *Notoplatypus* Lea (1 species from Australia); *Tesserocranulus* Schedl (1 species from Costa Rica to Cayenne); *Tesserocerus* Saunders (=*Damicerus* Spinola, *Tesseroplatypus* Schedl, *Tesserocephalus* Schedl) (30 species from southern Mexico to Argentina); *Spathidicerus* Chapuis (7 species from Sumatra to Philippines and New Guinea); *Periommatus* Chapuis (=*Asetus* Nunberg, *Setanus* Nunberg) (52 species from tropical Africa); *Chaetastus* Nunberg (=*Symmerus* Chapuis) (7 species from tropical Africa); *Cenocephalus* Chapuis (13 species from southern Mexico and Hispanola to Brazil); and *Mitosoma* Chapuis (=*Platypicerus* Nunberg, *Coccephalonus* Schedl) (26 species from Madagascar).

Schedl (1972) did not recognize the Tesserocerinae as a subfamily, but fragmented the group into his Diaporinae [*sic*], Periommatinae, and Platypodinae.

PLATYPODINAE

Introduced here are radical changes in the classification of Platypodinae that were found too late for inclusion in Wood & Bright (c1992). Foremost among these is the abandonment of the genus "sektionen" of Chapuis (1865), Strohmeyer (1912, 1914b), and Schedl (1972). This non-Linnaean category was apparently below the rank of subgenus but above the rank of species and was used liberally by Schedl with little objectivity. These "sektionen" are here replaced by a new classification of genera.

The Platypodinae, as presented here, appear to represent a recent, active, evolutionary explosion in which sharply delineated generic groups do not exist. For this reason all are placed in one tribe, Platypodini. Schedl's (1972:83) attempt to characterize his Crossotarsini as distinct from his Platypodinae was based on a character (sexual dimorphism of the protibiae) that did not occur throughout the group he attempted to characterize, nor was it limited to his Crossotarsini. Another set of characters was needed to divide his Platypodinae.

On the posterior portions of the metasternum and metepisternum of some Platypodini is a feeble to very strong, often glabrous impression for the reception of the metafemur. The anterior and lateral margins of this impression may be armed by (1) a continuous carina (African species) or (2) a series of minute spines (American species, with a few eastern hemisphere exceptions). Those Platypodini that lack this impression and its carina or spines also share other features generally not found in the other group. It should be mentioned that occasional females (American species) and about a dozen species allied to *Euplatypus longulus* (Chapuis) (all are American species) lack the impression and spines even though they (otherwise) clearly belong to the generic group with the impression and spines. Conversely, several of the largest species of *Crossotarsus* have one small, rounded nodule on the male metepisternum although they clearly belong to the generic group without the impression or spines. Among those groups treated here as genera that lack the impression and its armature, all (mostly females) that have mycetangia pores on the pronotum have numerous pores. Among those genera with the impression and spinelike armature, most of those species (primarily females) with mycetangia pores on the pronotum have only one pair, although a few large *Megaplatypus* have several, and the few

Baoocis with pores have many. All of those species with mycetangia pores on the pronotum and also with a carina on the metasternum-metepisternum impression (African species) have many pores.

Platypus Herbst

The genus *Platypus* Herbst (=*Cylindra* Illiger, *Stenoplatypus* Strohmeyer, *Platypinus* Schedl) as defined here is greatly reduced in the number of included species from that listed by Schedl (1972:169–242) and Wood & Bright (c1992). To these synonyms is added *Austroplatypus* Browne (1971:49), *new synonymy*. It also appears that *Dendroplatypus* Browne (1955:365) belongs here (only females were available for study). *Neotrachyostus quadrilobus* (Blandford) is here transferred from *Neotrachyostus* back to *Platypus*. *Platypus taxicornis* Schedl belongs here, not in *Treptoplatypus* where it was placed by Schedl (1972:245).

DESCRIPTION.—*Platypus* Herbst is a member of the Platypodini, as defined in the above key to genera, in which the posterior portions of the metasternum and metepisternum are not impressed or armed (key couplet 18a) and the protibiae are not sexually dimorphic (key couplet 19a). The male sutural apex on the elytral declivity is not dehiscent. Mycetangia pores when present on the pronotum (mostly females) are numerous.

CONTENTS.—Included here in this group are the following "sektionen" of *Platypus* as listed by Schedl (1972:169–242): *Platypi apicali* (1 sp., Fiji), *Platypi geminati* (3 spp., New Guinea), *Platypi hirtelli* (22 spp., India to Australia and Philippines), *Platypi lunati* (15 spp., India to Australia), *Platypi mesoadjuncti* (3 spp., Malaya to New Guinea), *Platypi paraspinulosi* (5 spp., Africa), *Platypi pseudospinulosi* (12 spp., Malaya and China to New Guinea), *Platypi punctati* (2 spp., India to New Guinea), *Platypi semiopaci* (9 spp., Australia to New Guinea), *Platypi spinulosi* (13 spp., Africa), *Platypi sulcati* (60 spp., Europe, India, and Japan to Australia). This reduces the 808 species of *Platypus* listed in Wood & Bright (c1992) to 121 species.

DISTRIBUTION.—Europe and Africa to Japan and Australia. 1 species (*quadrilobus* Blandford) of dubious affinity in Costa Rica.

Treptoplatypus Schedl

The genus *Treptoplatypus* Schedl was based on *Crossotarsus trepanatus* Chapuis. Schedl (1972:245) also included *circulicauda* Browne, *fischeri* Strohmeyer, *multiporus* Schedl, *quadriporus* Schedl, and *subaplanatus* Schedl, all (five) of which are unknown to me. As indicated above, *Treptoplatypus taxicornus* (Schedl) is here transferred back to *Platypus*.

DESCRIPTION.—A member of the Platypodini near *Platypus*, *Treptoplatypus* is distinguished by the strongly narrowed male elytral declivity that is rather abruptly, obliquely truncate and dehiscent at the sutural apex. The male elytral apex is usually strongly attenuate, and the male declivity is usually concave. Mycetangia pores on the female pronotum are numerous.

CONTENTS.—In addition to *trepanatus*, I here transfer from *Platypus* to *Treptoplatypus* the species *abietis* (Wood), *australis* (Chapuis), *biflexuosus* (Schedl), *micurus* (Schedl), *solidus* (Walker), and *wilsoni* (Swaine). It is probable that some (not all) species placed by Schedl (1972:197–199) in *Platypi oxyuri* should also be transferred here, as well as *longipennis* Montrouzier (Schedl 1972:196). Additional studies are needed to determine exactly which species should and should not be added to this genus.

DISTRIBUTION.—India and Japan to Australia and NW North America.

Peroplatypus, n. g.

DIAGNOSIS.—This genus is a member of the Platypodini near *Treptoplatypus*, but it is distinguished from that genus by the broad elytral declivity that is obliquely truncate, with the suture entire (slightly dehiscent in one species). It is distinguished from *Dinoplatypus* by the absence of an elytral constriction immediately cephalad from the declivity, and by the presence of setae on the face of the male declivity.

DESCRIPTION.—Metasternum and metepisternum without an impression or armature for reception of the metatibia. The male elytral declivity is broadly, obliquely truncate, not preceded by a transverse constriction; the suture is entire (one slight exception); the declivital face is ornamented by setae (either hairlike or scalelike); the costa at the base of the male declivity is obtuse to subacute, and the interstrial rows are sometimes indicated on the upper portion. The male declivital face is usually dull (shining in one species).

CONTENTS.—Type-species: *Platypus truncatipennis* Schedl. Included here are the *Platypi sulcato-truncati* (5 spp., Borneo, New Guinea) and *Platypi truncatipenni* (6 spp., Borneo, Sumatra, New Guinea) of Schedl (1972:211–212). Of these, only *platypoides* (Browne), *truncaticauda* (Schedl), *truncatigranosus* (Schedl), and *truncatipennis* (Schedl) were at hand for study.

DISTRIBUTION.—Malaya to New Guinea.

Dinoplatypus, n. g.

DIAGNOSIS.—The genus *Dinoplatypus* is distinguished from *Peroplatypus* Wood, above, by the subvertical, obliquely truncate male elytral declivity with the sutural apex modestly to very strongly, very broadly emarginate, and with the subvertical face moderately to strongly concave, brightly shining, and without punctures or setae; the upper margin of the male declivital face is usually acute, and there is a distinct constriction immediately cephalad from its base.

DESCRIPTION.—The male elytral declivity is subvertically truncate; its upper margin is acute; its face is broadly, subcircularly concave; its surface is brightly shining, impunctate, glabrous, with a substantial, often elaborate, emargination at the sutural apex. The male declivity has a distinct, transverse constriction immediately cephalad from its base. The female pronotum has numerous mycetangia pores.

CONTENTS.—Type-species: *Platypus cupulatus* Chapuis. Included here are the *Platypi cupulati* (29 spp.) of Schedl (1972:208–211).

DISTRIBUTION.—India and Japan to Australia and Micronesia.

Crossotarsus Chapuis

The genus *Crossotarsus* Chapuis, as treated here, is essentially as listed in Schedl (1972:96–112) and Wood & Bright (c1992), although it may become necessary to add to it all or part of *Carchesiopygus* Schedl (not seen) and *Crossotarsinulus* Schedl (not seen).

DESCRIPTION.—*Crossotarsus* is a member of the Platypodini, near *Platypus*, except that (key couplet 19) the protibiae are sexually dimorphic (male with the usual transverse rugae, female with most of the basal rugae replaced by confused granules). The male declivity is moderately reduced to almost absent (a row of dorsoventrally flattened spines arms its basal margin); the abdomen ascends rather strongly to meet the apex. The males of several of the larger species have a rounded nodule on the metepisternum. The female pronotum has numerous mycetangia pores.

CONTENTS.—Included here are the following groups as listed by Schedl (1972:96–112): *Crossotarsi alternante-depressi* (1 sp., Philippines), *Crossotarsi angulati* (4 spp., India, Japan, New Guinea), *Crossotarsi barbati* (11 spp., Malaya to Philippines and Australia), *Crossotarsi coleoptrati* (12 spp., India to Japan and New Guinea), *Crossotarsi subdepressi* (20 spp., India to Taiwan and Australia), *Crossotarsi genuini* (20 spp., India to Philippines and Australia), *Crossotarsi nitiduli* (4 spp., Malaya to New Guinea), *Crossotarsi ventricorni* (14 spp., India to Japan and New Guinea), *Crossotarsi incertae sedis* (3 spp., Java to Philippines, 1 sp. of doubtful affinity in Africa).

DISTRIBUTION.—India to Japan and Australia, *externedentatus* has extended its range through modern commerce to Hawaii and has been intercepted in additional areas.

Trachyostus Schedl

This genus is allied to *Crossotarsus*, but it is confined to Africa and Madagascar.

DESCRIPTION.—*Trachyostus* is allied to *Crossotarsus* as indicated by the similarly sexually dimorphic protibiae. The male elytral declivity is usually convex (rarely flattened), evenly rounded, never serrate or dentate, and the surface is usually dull. The venter of the abdomen ascends little, if any, to meet the elytral apex. Mycetangia pores are never present on the pronotum.

CONTENTS.—Included here are the 13 species from tropical Africa and Madagascar that were listed by Schedl (1972:88–89) and Wood & Bright (c1992).

DISTRIBUTION.—Tropical Africa and Madagascar.

Neotrachyostus Browne

The genus *Neotrachyostus* Browne, as used here, is essentially as listed in Schedl (1972:90–92) and Wood & Bright (c1992) except that *Platypus quadrilobus* Blandford is here transferred back to *Platypus*.

DESCRIPTION.—The sexually dimorphic protibiae of *Neotrachyostus* suggest a close relationship to *Trachyostus*. The male elytral declivital surface is never dull; it is variously impressed or excavated, with the ventrolateral margin serrate, dentate, or emarginate; its base is variously carinate or armed by spines. The female pronotum has one pair of mycetangia pores.

CONTENTS.—Schedl (1972:92) and Wood & Bright (c1992) list 14 species.

DISTRIBUTION.—Southern Mexico to Brazil.

Platyscapulus Schedl

The genus *Platyscapulus* Schedl (=*Platyscapus* Schedl 1939:397, 399, *Costaroplatus* Nunberg 1963:109) contains a group of American species formerly assigned to *Platypus*. *Platyscapulus* is here removed from synonymy with *Platypus* and is given full generic rank.

DESCRIPTION.—As defined here *Platyscapulus* contains those species formerly assigned to *Platypus* that have the metasternum-metepisternum impression armed on its anterior margin by a series of small spines and also have a pair of spines that arm visible male abdominal sternum 5 (Schedl 1972:195, fig. 49). The male elytral declivity is usually short, steep, and has the ventrolateral angles rather poorly developed, projecting little, if any. The male elytral interstriae are usually carinate on the posterior half of the disc. The pronotum never has mycetangia pores in either sex.

CONTENTS.—Included here are Schedl's (1972:235) *Platypi costellati* (13 spp., S Mexico to Brazil), *Platypi abdominales* (Schedl 1972:195) (3 spp., Costa Rica to Guyana), and *Platypi neocostellati* (Schedl 1972:195) (2 spp., Venezuela and Guyana to Brazil).

DISTRIBUTION.—Southern Mexico to Brazil.

Myoplatypus, n. g.

DIAGNOSIS.—This genus is distinguished from the closely allied *Oxyplatypus* Wood, below, by the occurrence of a pair of large spines on male visible abdominal sternum 4, and by the absence of spines on other sterna.

DESCRIPTION.—This genus is a member of the Platypodini that have a metasternum-metepisternum impression armed by small spines and a transverse pair of spines on male visible abdominal sternum 4. The pronotum usually has one pair of mycetangia pores in the female; they are sometimes present in the male.

CONTENTS.—Type-species: *Bostrichus flavicornis* Fabricius. Included here are *flavicornis* (Fabricius) (S USA to Cuba) and Schedl's (1972:220) *Platypi bilobati* (5 spp., Mexico to Costa Rica).

DISTRIBUTION.—Southeastern USA and Cuba to Mexico and Venezuela.

Oxoplatypus, n. g.

DIAGNOSIS.—This genus is a member of the Platypodini near *Platyscapulus*. It is distinguished from *Platyscapulus* by the presence of a transverse pair of large spines that arm male visible abdominal sternum 3, and by the absence of spines on sternum 5.

DESCRIPTION.—This genus is established to contain one known species. It is a representative of the Platypodini with the metasternum-metepisternum impression armed by small spines on the anterior margin, and male visible abdominal sternum 3 is armed by a transverse pair of large spines. The female pronotum bears one unusually large pair of mycetangia pores; the male pronotum is without pores.

CONTENTS.—Type-species: *Scolytus quadridentatus* Olivier. One species is known, *quadridentatus* (Olivier) (=*blanchardi* Chapuis, *disciporus* Chapuis).

DISTRIBUTION.—Southeastern USA to northern Mexico, in *Quercus* spp.

Platyphysus, n. g.

DIAGNOSIS.—This genus is a member of the Platypodini having the metasternum-metepisternum impression armed on its anterior margin by small spines, but none of the visible male abdominal sterna is armed by spines. *Platyphysus* is distinguished from allied genera by the strongly convex, steep male elytral declivity that is almost unarmed, and by the horizontal venter of the abdomen with visible sternum 5 inflated, its posterior one-fourth ascending rather abruptly to meet the apex of the elytra.

DESCRIPTION.—In this genus visible male abdominal sternum 5 is strongly inflated (moderate in female), with its posterior one-fourth ascending to meet the apex of the elytra. The elytral declivity is convex, steep, and descends further than in related genera; male armature is sparse and rather small. The metasternum-metepisternum impression is armed by small spines as in related genera.

Contents.—Type-species: *Platypus obtusus* Chapuis. Also included here are Schedl's (1972:187) *Platypi declivi* (4 spp., Brazil) and *Platypus pouteriae* Wood.

Distribution.—Costa Rica to Venezuela, in *Pouteria* spp.

Megaplatypus, n. g.

Diagnosis.—This large group of American species, formerly placed in *Platypus*, is diverse and is distinguished with some difficulty. From *Euplatypus* Wood, below, it is distinguished by the more poorly formed and much less strongly produced posterolateral angles of the male elytra (key couplet 31); one or two pairs of small denticles sometimes arm the apical margin between these angles. Mycetangia pores are uncommon (female) or rare (male) but may consist of one pair or a pair of clusters of pores (perhaps 4 to 12 on each side).

Description.—This is a genus of Platypodini having the metasternum-metepisternum impression armed by small spines; they lack spines on the visible male abdominal sterna. The male declivity descends at least half the distance to meet the abdomen, its lateral angles are rather poorly produced (usually they do not exceed the apex of the suture), and the apical margin between these angles sometimes is armed by one or two pairs of small denticles. The pronotum usually is without mycetangia pores, but one pair or multiple pores are sometimes present (particularly in the female).

Contents.—Type-species: *Platypus dentatus* Dalman. Also included here are Schedl's (1972:238-242) *Platypi plicati* (82 spp., S Mexico to Argentina), Schedl's (1972:186–189) *Platypi discoidales* (4 spp., S Mexico to Brazil), Schedl's (1972:184) *Platypi punctatosulcati* (1 sp., Guatemala to Panama), Schedl's (1972:229) *Platypi pseudocaudati* (4 spp., Guyana to Brazil), *Platypus nudatus* Wood (Colombia), *P. pernudus* Schedl (Guyana), and *P. simpliciformis* Wood (Costa Rica).

Distribution.—Mexico to Argentina.

Euplatypus, n. g.

Diagnosis.—This genus is distinguished from *Megaplatypus* Wood, above, by the much more strongly produced ventrolateral angles of the male declivity that exceed the level of the sutural apex.

Description.—This genus is a member of the Platypodini having the metasternum-metepisternum impression armed on its anterior margin by small spines. None of the visible abdominal sterna are armed by spines. The male ventrolateral angles of the declivity are extended caudad into a pair of processes that exceed the sutural apex (apices of each of these processes are usually bi- or tridentate, and never with serrations or denticles on the apical margin between these processes). The pronotum often has one pair of mycetangia pores in the female or in both sexes.

Contents.—Type-species: *Bostrichus parallelus* Fabricius. Also included here are Schedl's (1972:230–234) *Platypi trispinati* (39 spp., USA to Argentina, Madagascar, tropical Africa, Australia, Sri Lanka, etc.) and Schedl's (1972:205) *Platypi caudati* (19 spp., S Mexico to Argentina). Some of the *caudati* group from tropical America lack the small spines that arm the metasternum-metepisternum impression in one or both sexes.

Distribution.—Southern USA to Argentina, a few in Africa, Madagascar. *Euplatypus parallelus* (Fabricius) has been carried through modern commerce worldwide in tropical areas (Wood & Bright c1992, 1664–1668). It has also been intercepted in Australia and India in recent months.

Baiocis Browne

The genus *Baiocis* Browne as treated here is essentially as it was established by Browne (1962:651) and listed by Wood & Bright (c1992), except that *Platypus kuntzeni* Schedl apparently belongs in *Crossotarsus*.

Description.—This genus is a member of the Platypodini having the metasternum-metepisternum impression armed on its anterior margin by small spines. The species are small, usually reticulate, very slender, with sexual dimorphism obscure. The male elytral declivity is unarmed and it descends feebly, if at all. The visible male abdominal sternum 5 is concave. Mycetangia pores, when present on the pronotum, are numerous.

Distribution.—Australia to Malaya.

Epiplatypus, n. g.

Diagnosis.—This genus is a member of the Platypodini having the metasternum-metepisternum impression armed by small spines on its anterior margin. It is distinguished in the male from *Megaplatypus* Wood, above, and *Teloplatypus* Wood, below, by the unique structure of the male elytral declivity.

Description.—This genus is allied to *Teloplatypus* but is distinguished by the presence of two pairs of serrations on the ventrolateral margin of the male elytral declivity; these serrations are usually connected by a carina; the median pair (often both pairs) is on the apical margin. One pair of mycetangia pores is often present on the female pronotum or on both sexes.

Contents.—Type-species: *Platypus desceptor* Wood. Also included here are *Platypus annexus* Wood, *P. applanatus* Wood, *P. deplanatus* Wood, *P. eugestus* Wood, *P. eximius* Wood, *P. filaris* Wood, *P. jamacensis* Bright, *P. secus* Wood, *P. spectus* Wood, *P. vegestus* Wood, and apparently most of Schedl's (1972:213–214) *Platypi complanati*.

Distribution.—Costa Rica to Brazil.

Teloplatypus, n. g.

Diagnosis.—This genus is distinguished from *Epiplatypus* Wood, above, by the unique structure of the male elytral declivity as defined in the above key to genera.

Description.—This genus is a member of the Platypodini having the metasternum-metepisternum impression armed on its anterior margin by small spines. The male elytral declivity has only one pair of serrations on the ventrolateral margin, with a carina extending dorsad from this spine to a spine on interstriae 3 located at the base of the declivity; the declivity descends only slightly, and its basal margin is usually armed by small spines on interstriae 1, 3, and 5. Mycetangia pores are never present on the pronotum in either sex.

Contents.—Type-species: *Platypus concinnus* Blandford. Included here is Schedl's (1972:218–219) *Platypi terminati* (16 spp.).

Distribution.—Southern Mexico to Argentina.

Cylindopalpus Strohmeyer

The genus *Cylindropalpus* Strohmeyer, as treated here, is essentially as listed by Browne (1962:650, 655), Schedl (1972:131–134), and Wood & Bright (c1992).

Description.—This genus is a member of the Platypodini having the anterior margin of the metasternum-metepisternum impression continuously costate. The abdomen ascends gradually and moderately to meet the elytra. The male visible abdominal sterna are transversely convex, sternum 2 is not enlarged or modified. The male elytral declivity is convex; moderately steep, and with tubercles small and inconspicuous. The female frons is broad and shallowly to moderately concave.

Contents.—Wood & Bright (c1992) list 14 species.

Distribution.—Africa to Madagascar.

Triozastus Schedl

The genus *Triozastus* Schedl, as treated here, is essentially as listed by Schedl (1972:246–248) and Wood & Bright (c1992). There appears to be considerable confusion in this genus on how to interpret individual and populational variability into taxonomic categories.

Description.—This genus is distinguished from *Cylindropalpus* Strohmeyer by the male abdomen being broadly concave (both transversely and longitudinally) from the base of visible sternum 1 to the apex of 5, this concave area being often elaborately pubescent. The male elytral declivity descends only slightly, and its basal margin is armed by spines; interstriae 1 near its apex diverges laterad moderately then descends slightly before its apex. The female frons bears a pair of small to rather large concavities in the lateral areas between the bases of the mandibles and the antennal insertions.

Contents.—Wood & Bright (c1992) list 7 species.

Distribution.—Tropical Africa.

Mesoplatypus Strohmeyer

As treated here, the genus *Mesoplatypus* Strohmeyer is based on Wood & Bright (c1992) and on Schedl (1972:165–168).

Description.—This genus is a member of that portion of the Platypodini having a costate anterior margin of the metasternum-metepisternum impression and having visible male abdominal sterna 2, 3, or 4 armed by spines. In some members male sternum 2 bears at least a partial transverse carina that is reminiscent of *Doliopygus*. The female frons is concavely impressed (in all species?).

Contents.—Wood & Bright (c1992) list 17 species.

DISTRIBUTION.—Tropical Africa.

Doliopygus Schedl

The genus *Doliopygus* Schedl (=*Scutopygus* Nunberg, *Pygodolius* Nunberg, *Mixopygus* Nunberg, *Mesopygus* Nunberg), as treated here, is essentially as listed by Schedl (1972:143–164) and by Wood & Bright (c1992).

DESCRIPTION.—This genus is allied to *Mesoplatypus* Strohmeyer but is sharply distinguished by characters of the male abdomen. Male visible abdominal sternum 2 has a strongly developed, transverse carina that is sometimes divided at the median line. The sternum caudad from this carina ascends abruptly in union with sterna 3, 4, and 5 to form a subvertical, strongly concave, subcircular face that functions in the removal of frass from the gallery entrance hole. The male declivity is reduced to obsolete; its basal margin is armed by a row of dorsoventrally flattened costae (derived from spines) that are interrupted at the strial intervals. The female frons is variously sculptured and may be elaborately ornamented by setae in some species. Mycetangia pores on the pronotum are absent.

CONTENTS.—Wood & Bright (c1992) list 142 species.

DISTRIBUTION.—Tropical Africa.

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PARTIAL CHECKLIST OF PLATYPODINAE

As an aid to the interpretation of the above changes, the following list of valid names in Platypodinae is presented. Only valid generic and specific names are included. Synonyms and other subfamilies and genera not included here are listed in Wood & Bright (1992).

Platypus
- *andrewesi* Strohmeyer
- *apicalis* White
- *arduus* Schedl
- *arisanensis* Murayama
- *arrogans* Schedl
- *bajulus* Schedl
- *balanocarpus* Schedl
- *barbatulus* Schedl
- *beilschmiediae* Schedl
- *biconiger* Schedl
- *biformis* Chapuis
- *bihamatus* Schedl
- *caryophyllatus* Schedl
- *conjunctus* Schedl
- *cornutus* Schedl
- *crassus* Strohmeyer
- *curtus* Chapuis
- *cylindrus* (Fabricius)
- *darjeelingensis* Schedl
- *diffidens* Schedl
- *dignus* Schedl
- *effetus* Schedl
- *emdeni* Schedl
- *enormis* Schedl
- *fracticostis* Schedl
- *fulmeki* Schedl
- *geminatus* Chapuis
- *gerstaeckeri* Chapuis
- *grayi* Schedl
- *hinchinachara* Schedl
- *hirtellus* Schedl
- *histrix* Schedl
- *horishensis* Murayama
- *hybridus* Schedl
- *impressus* Strohmeyer
- *inermis* Sampson
- *insularis* Strohmeyer
- *intermedius* Schedl
- *jansoni* Chapuis
- *juvencus* Schedl
- *kalshoveni* Schedl
- *kinshuensis* Murayama
- *klapperichi* Schedl
- *latedeclivis* Schedl
- *lineellus* Schedl
- *lucasi* Chapuis
- *lunatipennis* Schedl
- *lunifer* Schedl
- *luzonicus* Schedl
- *minutissimus* Schedl
- *mjobergi* Schedl
- *modestus* Blandford
- *morigerus* Schedl
- *multiporus* Schedl
- *neoplicatus* Schedl
- *niijimai* Murayama
- *obtusipennis* Schedl
- *omissus* Schedl
- *opacideclivis* Schedl
- *opacifrons* Schedl
- *orientalis* Strohmeyer
- *ornaticeps* Schedl
- *ovatus* Strohmeyer
- *pahangensis* Schedl
- *partitus* Schedl
- *pasaniae* Schedl
- *pedum* Sampson
- *pennatus* Schedl
- *perrisi* Chapuis
- *picinus* Schedl
- *politus* Chapuis
- *porcellus* Schedl
- *praeteritus* Schedl
- *pseudocurtus* Schedl
- *pseudoselysi* Schedl
- *puerulus* Schedl
- *quadricinctus* Schedl
- *queenslandi* Schedl
- *quercicola* Schedl
- *quercinus* Schedl
- *quercivorus* Murayama
- *rimulosus* Schedl
- *rufescens* Strohmeyer
- *sampsoni* (Schedl)
- *schenklingi* (Strohmeyer)
- *secretus* Sampson
- *selysi* Chapuis
- *semiermis* Schedl
- *semigranosus* (Sampson)
- *semiopacus* Strohmeyer
- *setaceus* Chapuis
- *sexporus* (Schedl)
- *sexualis* Beeson
- *shillongensis* Schedl
- *signatus* Chapuis
- *simulans* Schedl
- *sinensis* Schedl
- *singalangensis* Schedl
- *spectabilis* Schedl
- *spinulosus* Strohmeyer
- *striatopunctatus* Schedl
- *subdepressus* Schedl
- *subgranosus* Schedl
- *subplicatus* Schedl
- *subsecretus* Browne
- *subsidarius* Schedl
- *subsimilis* Schedl
- *suffodiens* Sampson
- *tasmanicus* Schedl
- *taxicornis* Schedl
- *tayabasi* Schedl
- *tenellus* Schedl
- *terebrans* Schedl

uniformis Schedl
utibilis (Schedl)
verelunatus (Beeson)
vesculus Schedl
vethi Strohmeyer
vetulus Schedl
webberi Schedl
westwoodi Chapuis

Treptoplatypus
abietis (Wood)
australis (Chapuis)
biflexuosus (Schedl)
circulicauda Browne
fischeri (Strohmeyer)
micrurus (Schedl)
multiporus Schedl
quadriporus Schedl
solidus (Walker)
subaplanatus (Schedl)
trepanatus (Chapuis)
wilsoni (Swaine)

Peroplatypus
abruptus (Sampson)
fallax (Schedl)
laosi (Schedl)
lawasensis (Browne)
obliquecaudatus (Schedl)
platypoides (Browne)
retusipennis (Schedl)
semisulcatus (Schedl)
truncaticauda (Schedl)
truncatigranosus (Schedl)
truncatipennis (Schedl)

Dinoplatypus
acutidentatus (Murayama)
aduncus (Chapuis)
agnatus (Schedl)
algosus (Schedl)
anthocephali (Schedl)
biuncus (Blandford)
calamus (Blandford)
carus (Strohmeyer)
chevrolati (Chapuis)
cupulatulus (Schedl)
cupulatus (Chapuis)
decens (Sampson)
falcatus (Strohmeyer)
forficula (Chapuis)
hamatus (Blandford)
lepidus (Chapuis)
luniger (Motschulsky)
malaisei (Schedl)
maritimus (Schedl)
noonadanae (Browne)
omega (Schedl)
pallidus (Chapuis)
piniperda (Schedl)
pseudocupulatus (Schedl)
tenuis (Murayama)
tenuissimus (Schedl)
tetracerus (Beeson)
umbraticus (Schedl)
uncinatus (Blandford)

Crossotarsus
See Wood & Bright (1992:1195–1209)

Carchesiopygus
See Wood & Bright (1992:1209–1210)

Crossotarsinulus
See Wood & Bright (1992:1210)

Trachyostus
See Wood & Bright (1992:1210–1213)

Neotrachyostus
See Wood & Bright (1992:1213–1214)

Platyscapulus
abditulus Wood
abditus (Schedl)
carinulatus Chapuis
clunalis Wood
cluniculus (Wood)
clunis (Wood)
costellatus Schedl
frontalis (Blandford)
imitatrix Schedl
manus Schedl
occipitis Wood
pulchellus Chapuis
pulcher (Chapuis)
pusillimus Chapuis
shenefelti Nunberg
subabditus (Schedl)
turgifrons (Schedl)
umbrosus (Schedl)

Myoplatypus
biporus (Blandford)
brevicornis Wood
connexus Wood
flavicornis Fabricius
prenexus Wood
senexus Wood

Oxoplatypus
quadridentatus Olivier

Platyphysus
convexus Schedl
laticollis Chapuis
obtusus Chapuis
pouteriae Wood
ronfabri Reichardt

Megaplatypus
artecarinatus Schedl
attentus Schedl
auricularis Chapuis
auritus Chapuis
batesi Chapuis
bicornis Nunberg
bidens Schedl
binodulus Chapuis
brevicaudatus Nunberg
caracanus Schedl
carinifer Schedl
chiriquensis Wood

[illegible] (Schedl)
[illegible] (Schedl)
[illegible] (Chapuis)
[illegible] (Schedl)
curvidens (Schedl)
darlingtoni (Reichardt)
dentatus (Dalman)
[illegible] (Schedl)
[illegible] (Chapuis)
[illegible] (Chapuis)
discicollis (Chapuis)
discoidalis (Schedl)
distinguendis (Schedl)
dolobratus (Blandford)
durus (Schedl)
egregius (Schedl)
elongatus (Chapuis)
equadorensis (Schedl)
exaratus (Blandford)
exitialis (Wood)
exitiosus (Schedl)
flexiosus (Schedl)
fossulatus (Chapuis)
fragosus (Scheld)
fuscus (Chapuis)
godmani (Blandford)
granarius (Schedl)
gregalis (Schedl)
holdhausi (Schedl)
ignotus (Schedl)
imporcatus (Blandford)
insidiosus (Schedl)
insignatus (Schedl)
inviolatus (Schedl)
irregularis (Schedl)
irrepertus (Schedl)
irruptus (Schedl)
jelskii (Nunberg)
konincki (Chapuis)
lafertei (Chapuis)
latreillei (Chapuis)
limbatus (Chapuis)
liraticus (Wood)
liratus (Blandford)
luridus (Chapuis)
malignus (Schedl)
marginatus (Chapuis)
mutatus (Chapuis)
navarrodeandradei (Marelli)
neglectus (Schedl)
nitidicollis (Schedl)
oculatus (Wood)
[illegible] (Blandford)
[illegible] (Chapuis)
[illegible] (Chapuis)
[illegible] (Schedl)
[illegible] (Schedl)
[illegible] (Schedl)
[illegible] (Schedl)
peruanus (Nunberg)
porrectus (Chapuis)
pseudodignatus (Schedl)
pseudoplicatus (Schedl)
quaesitus (Schedl)
[illegible]costatus (Chapuis)
[illegible] (Schedl)
raucus (Schedl)
reichei (Chapuis)
robustus (Chapuis)
salvini (Blandford)
schmidti (Chapuis)
sexcostatus (Chapuis)
simpliciformis (Wood)
sobrinus (Schedl)
suavifer (Schedl)
suboblitaratus (Schedl)
subsulcatus (Chapuis)
tiriosensis (Reichardt)
tuberculatus (Chapuis)
umbonatus (Blandford)
ursinus (Schedl)
ursus (Schedl)

Euplatypus
aequalicinctus (Schedl)
alienus (Schedl)
alternans (Chapuis)
angustatulus (Wood)
angustatus (Chapuis)
angustioris (Schedl)
araucariae (Schedl)
areolatus (Schedl)
bellus (Schedl)
bilobatus (Strohmeyer)
compositus (Say)
contextus (Schedl)
coronatus (Schedl)
costaricensis (Schedl)
cribricollis (Blandford)
cuspidatus (Schedl)
decorus (Schedl)
dignatus (Schedl)
dimidiatus (Chapuis)
dissimilis (Chapuis)
dissipabilis (Schedl)
efferatus (Schedl)
haagi (Chapuis)
hians (Chapuis)
hintzi (Schaufuss)
immunis (Schedl)
laminatus (Schedl)
longior (Wood)
longius (Wood)
longulus (Chapuis)
madagascariensis (Chapuis)
minusculus (Schedl)
mulsanti (Chapuis)
otiosus (Schedl)
parallelus (Fabricius)
patulus (Chapuis)
perminiicus (Schedl)
pertusus (Chapuis)
pini (Hopkins)
porosus (Blandford)
pseudolongulus (Schedl)
pulicaris (Chapuis)
roberti (Chapuis)
rugosifrons (Schedl)
santacruzensis (Mutchler)
segnis (Chapuis)
simpliciformis (Wood)
sinuosus (Chapuis)

solutus (Chapuis)
striatus (Chapuis)
tragus (Schedl)
tricuspidatus (Schedl)
trispinatulus (Schedl)
trispinatus (Schedl)
truncatus (Chapuis)
vicinus (Blandford)

Baiocis
See Wood & Bright c1992:1215–1217

Epiplatypus
adnexus (Schedl)
annexus (Wood)
applanatus (Wood)
brasiliensis (Nunberg)
complanatus (Schedl)
deceptor (Wood)
deplanatus (Wood)
discolor (Blandford)
eugestus (Wood)
eximius (Wood)
filaris (Wood)
guadeloupensis (Schedl)
jamaicensis (Bright)
nudus (Schedl)
pernudus (Schedl)
secus (Wood)
spectus (Wood)
vegestus (Wood)

Teloplatypus
brunneus (Chapuis)
carinifrons (Schedl)
collatatus (Schedl)
concinnulus (Blandford)
cunxus (Schedl)
excisus (Chapuis)
humilis (Chapuis)
inaccessus (Schedl)
marcidus (Blandford)
ornatus (Schedl)
pallidipennis (Blandford)
percomis (Schedl)
perdiligens (Schedl)
ratzeburgi (Chapuis)
striatopennis (Schedl)
subitarius (Schedl)
ustulatus (Chapuis)

Cylindropalpus
See Wood & Bright c1992:1217–1219

Triozastus
See Wood & Bright c1992:1219–1221

Mesoplatypus
See Wood & Bright c1992:1221–1223

Doliopygus
See Wood & Bright c1992:1223–1240

Spathicranuloides
See Wood & Bright c1992:1210

Dendroplatypus
See Wood & Bright c1992:1240

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SIMULATION MODELING OF AMERICAN MARTEN (*MARTES AMERICANA*) POPULATIONS: VULNERABILITY TO EXTINCTION

Robert C. Lacy[1] and Tim W. Clark[2]

ABSTRACT.— American marten (*Martes americana*) are medium-sized mammalian carnivores inhabiting forest communities across northern North America. Martens are susceptible to local extinction from habitat alterations, trapping, and other factors. We (RCL) developed a population model called VORTEX to estimate extinction probabilities for marten populations as a management tool. The model permits managers to simulate various levels of timber harvesting, commercial trapping, and other factors to estimate their effects on marten populations. This paper describes this model and illustrates its benefits by using marten data from the Greater Yellowstone Ecosystem of northwestern Wyoming. Results are preliminary. Populations of 50 and 100 martens were simulated. The most optimistic scenario with populations of 100 individuals, no trapping, no logging, and no migrants showed a probability (66%) of surviving 100 years. Extinction probabilities were sensitive to immigration and emigration rates. Numerous scenarios were simulated and showed a range of results. Results of population viability analysis can be translated into area requirements if densities are known or can be estimated. In turn, various habitat patches and interconnecting corridors can be examined for their ability to support viable marten populations. Population modeling is invaluable to "adaptive management" of martens as well as other species.

Key words: adaptive management, American marten, demographic stochasticity, environmental variation, genetic variation, extinction, Greater Yellowstone Ecosystem, Population Viability Analysis, simulation modeling, wildlife conservation, Martes americana.

American marten populations are susceptible to local extinction from habitat alterations, trapping, and other factors. For this reason and because martens are sometimes considered an "indicator species" under the National Forest Management Act of 1976 by the U.S. Forest Service, it is important to have a means of estimating extinction probabilities for marten populations as a management tool. We developed such a means, a computer simulation model called VORTEX, that allows managers to carry out a population vulnerability assessment (Lacy 1993). This simulation permits managers to vary levels of timber harvesting, commercial trapping, and other factors and estimate their effects on marten populations. Population management targets can be explored with this procedure and, in the field, marten populations maintained that ensure their persistence in the face of foreseeable extinction pressures (e.g., habitat fragmentation). This paper describes this model and illustrates its utility in marten conservation and management.

The results presented in this paper are preliminary. They draw largely on marten population data and environmental conditions in the Greater Yellowstone Ecosystem of northwestern Wyoming (Clark et al. 1989 [Demographic characteristics], Clark et al. 1989 [American marten]). The model can be rerun with better data from this area or data from other regions to estimate population vulnerability to local extinction under various conditions. This model has been used on a variety of rare and endangered species worldwide and has directly aided their conservation and management (e.g., Lacy et al. 1989, Seal and Lacy 1989, Lacy and Clark 1990, Maguire et al. 1990, Seal and Lacy 1990, Lindenmayer et al. 1991, Lindenmayer et al. in press). We are confident it can aid American marten conservation and management too.

EXTINCTION PROCESS

To understand how VORTEX works, one must first understand the extinction process (see Shaffer 1981, Gilpin and Soulé 1986, Clark et al. 1990 [Management]). As populations become fragmented and reduced in size, random fluctuations in population size can

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become more important determinants of persistence than whether mean population growth is positive. Four classes of factors affect marten population survival: demographic, environmental, catastrophic, and genetic variation. Fluctuations in population size can result from any or all of these four kinds of stochastic (random) effects.

Demographic variation results from the probabilistic nature of birth and death processes: Even if the probability of an animal reproducing or dying is always constant, we expect that the actual proportion reproducing or dying within any time interval will vary according to a binomial distribution with mean equal to the probability of the event (p) and variance given by $V = p * (1 - p) / N$. Demographic variation is thus intrinsic to the population and occurs because birth and death events are determined by random processes.

Environmental variation (EV) is the variation in the probabilities of reproduction and mortality that occur because of changes in the environment on an annual basis or other time scales. Thus, EV impacts all individuals in the population simultaneously, changing the probabilities (means of the above binomial distributions) of birth and death. The sources of EV are thus extrinsic to the population itself, due to weather, predator and prey populations, parasite loads, etc.

At the extreme of environmental variation are events that could be termed catastrophes. Epidemic diseases, severe storms, forest fires, or floods might kill a substantial portion of individuals in a population or disrupt a breeding season. Such events can impact a population more severely than could be predicted from the normal range of environmental variation in reproductive and mortality rates. Moreover, such catastrophes are often the proximate cause of the final extinction of local populations. Catastrophes are individually rare and unpredictable, but most populations observed over a number of decades are likely to suffer one or more events that would commonly be termed catastrophes.

The transmission of genes is also a random process, and genetic variability is lost from small populations due to drift and inbreeding. Inbreeding can cause decline in fecundity and survival, exacerbating demographic problems and leading populations more rapidly toward extinction (Wright 1977, Ralls and Ballou 1983, Ralls et al. 1988).

The combination of these random forces—demographic stochasticity, environmental variation, catastrophes, and genetic drift—destabilize small populations and mutually exacerbate the effects of each level of stochasticity. For example, the random loss of genetic variation that occurs as populations become small due to low fecundity and high mortality in turn causes further decreased fecundity, greater mortality, and susceptibility to environmental variation and catastrophes. The feedback among the various forces destabilizing small populations has been termed the "extinction vortex" (Gilpin and Soulé 1986).

POPULATION VIABILITY ANALYSIS

Population viability analysis (PVA) is a relatively recent procedure for estimating the viability of small populations of organisms (Shaffer 1981). Clark et al. (1990 [Population viability]:1) defined PVA as a "procedure that allows wildlife managers to simulate, using computer models, extinction processes that act on small populations, and therefore to assess their long term viability." In both real and simulated populations, a number of interacting demographic, environmental, catastrophic, and genetic processes determine the vulnerability of a population to extinction. Life table analyses yield average long-term projections of population growth (or decline) but do not reveal the fluctuations in population size that would result from stochastic processes. Computer models can simulate the four interacting types of extinction processes, and the effects of both deterministic and stochastic forces can be explored. By using this procedure, one can also simulate the outcome of alternative management options, such as maintaining habitat or increasing it, reducing mortality, supplementing the population, or other management options. As a result, PVA gives managers a powerful tool to aid in determining the vulnerability of populations and in setting management targets. PVA is especially useful for managing rare and endangered species (Clark et al. 1989 [Designing and managing], Clark et al. 1990 [Management], Clark et al. 1990 [Population viability]).

PVA also provides quantitative predictions of population growth, demographic fluctuations, and decay of genetic variation, based on explicitly stated assumptions. Thus, PVA can provide both an explicit model of population dynamics and the testable predictions that are necessary to bring the projection and management of wildlife populations into the realm of falsifiable science. The outcome of management based on PVA can provide a test of the adequacy of our understanding of the population dynamics, by comparison of quantified predictions to population performance, while achieving the goals of the management plan. PVA has also been coupled with other analytical approaches, such as risk assessment and decision analysis, to better manage species populations (Maguire 1986, Maguire et al. 1990).

VORTEX: COMPUTER PROGRAM FOR MODELING POPULATION DYNAMICS

The complex interactions among demographic and genetic factors as they can impact populations of American martens were examined by computer simulation modeling, using the program VORTEX. VORTEX is a powerful, but user-friendly, program for modeling vertebrate population behavior by way of Monte Carlo simulation of demographic and genetic events in the history of the population (Lacy 1993). Some of the algorithms in VORTEX were taken from a simulation program, SPGPC, written in BASIC by James Grier of North Dakota State University (Grier 1980a, 1980b, Grier and Barclay 1988).

VORTEX models population processes as discrete, sequential events, with probabilistic outcomes. VORTEX simulates birth and death processes and the transmission of genes through the generations by generating random numbers to determine whether each animal lives or dies, whether each adult female produces litters of size 0, 1, 2, 3, 4, or 5 during each year, and which of the two alleles at a genetic locus are transmitted from each parent to each offspring. Mortality and reproduction probabilities are sex-specific. Fecundity is assumed to be independent of age (after an animal reaches reproductive age). Mortality rates are specified for each pre-reproductive age class and for reproductive-age animals. The mating system can be specified to be either monogamous or polygynous. In either case, the user can specify that only a subset of the adult male population is in the breeding pool (the remainder being excluded perhaps by social factors). Those males in the breeding pool all have equal probability of siring offspring.

Each simulation is started with a specified number of males and females of each pre-reproductive age class, and a specified number of males and females of breeding age. Each animal in the initial population is assigned two unique alleles at some hypothetical genetic locus, and the user specifies the severity of inbreeding depression (expressed in the model as an increase in juvenile mortality in inbred animals). The computer program simulates and tracks the fate of each population and then outputs summary statistics on the probability of population extinction over specified time intervals, the mean time to extinction of those simulated populations that went extinct, the mean size of populations not yet extinct, and the levels of genetic variation remaining in any extant populations.

A population carrying capacity is imposed by a probabilistic truncation of each age class if the population size after breeding exceeds the specified carrying capacity. The program allows the user to model trends in the carrying capacity as linear increases or decreases across a specified number of years.

VORTEX models environmental variation simplistically by selecting at the beginning of each year the population age-specific birth rates, age-specific death rates, and carrying capacity from distributions with means and standard deviations specified by the user. EV in birth and death rates is simulated by sampling binomial distributions, with the standard deviations specifying the annual fluctuations in probabilities of reproduction and mortality. EV in reproduction and EV in mortality can be specified to be acting independently or jointly (correlated in so far as is possible for discrete binomial distributions).

Unfortunately, rarely do we have sufficient field data to estimate the fluctuations in birth and death rates, and in carrying capacity, for a wild population. (The population would have to be monitored for long enough to separate, statistically, sampling error, demographic variation in the number of breeders and deaths, and annual variation in the probabilities of these events.) Lacking any data on annual variation, a user can try various values, or set

EV = 0 to model the fate of the population in the absence of any environmental variation.

VORTEX can model catastrophes, the extreme of environmental variation, as events that occur with some specified probability and reduce survival and reproduction for one year. A catastrophe is determined to occur if a randomly generated number between 0 and 1 is less than the probability of occurrence (i.e., a binomial process is simulated). If a catastrophe occurs, the probability of breeding is multiplied by a severity factor specified by the user. Similarly, the probability of surviving each age class is multiplied by a severity factor specified by the user.

VORTEX also allows the user to supplement or harvest the population for any number of years in each simulation. The numbers of immigrants and removals are specified by age and sex. These numbers of immigrants and removals are modeled as constants, not dependent on population size. VORTEX outputs the observed rate of population growth separately for the years of supplementation/harvest and for the years without such management, and allows for reporting of extinction probabilities and population sizes at whatever time interval is desired (e.g., summary statistics can be output at 5-year intervals in a 100-year simulation).

VORTEX can track multiple sub-populations, with user-specified migration among the units. The migration rates are entered for each pair of sub-populations as the proportion of animals in a sub-population that migrates to another sub-population (equivalently, the probability that an animal in one migrates to the other) each year. Because of migration (and, possibly, supplementation), there is the potential for population recolonization after local extinction. VORTEX tracks the time to first extinction, the time to recolonization, and the time to re-extinction.

Overall, the computer program simulates many of the complex levels of stochasticity that can affect a population. Because VORTEX is a detailed model of population dynamics, it is not practical to examine all possible factors and all interactions that may affect a population. It is therefore incumbent upon each user to specify those parameters that can be estimated reasonably, to leave out of the model those that are believed not to have a substantial impact on the population of interest, and to explore a range of possible values for parameters that are potentially important but very imprecisely known.

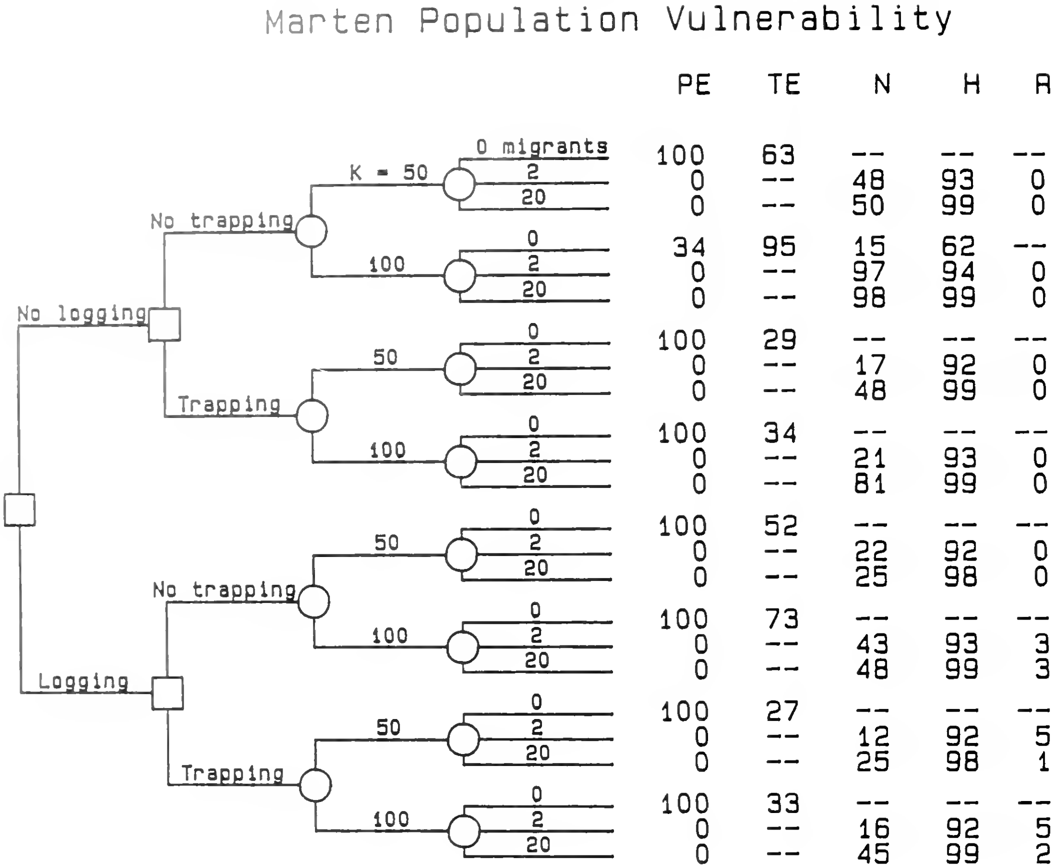
VORTEX is compiled for use on microcomputers running the MS-DOS (Microsoft Corp.) operating system. VORTEX and a manual describing its use are available from the office of the Captive Breeding Specialist Group (Species Survival Commission, IUCN), 12101 Johnny Cake Ridge Road, Apple Valley, Minnesota 55124. Descriptions of the program structure and underlying assumptions are given in Lacy (1993). Detailed descriptions of the algorithms used in VORTEX, as well as the source code (in the C programming language), are given in Lindenmayer et al. (1991).

POPULATION BIOLOGY PARAMETERS FOR MARTENS

We modeled a variety of scenarios of marten population behavior (Fig. 1). For these preliminary analyses, age of reproduction, mean birth and age-specific death rates, degree of polygyny, and sex ratio were obtained from published studies. Age of first reproduction (time at which females give birth to their first litters) was set at 2 years for females, following the report by Strickland et al. (1982) that 80% of yearling females (approximate age 16 months) usually become pregnant, giving birth about 8 months later. Although males sexually mature as yearlings also, we assumed that males usually do not breed successfully until a year later (their first offspring born when sires are about 3 years of age).

Litter sizes were assumed to be typically 3 (60% of adult females), but occasionally smaller (25% of adult females producing litters of 2, 10% producing litters of 1, and 5% not breeding in an average year). The mean litter size produced by the distribution used is 2.53 (mean fecundity of adult females = 2.40, considering also the 5% that fail to breed). The sex ratio at birth was assumed to be 1:1 (Clark et al. 1987).

Breeding males have been reported to have home ranges large enough to encompass the territories of three females (Clark et al. 1989 [American marten]), and we therefore assumed that the average successfully breeding male mates with three females. Given the differential mortality assumed to act on the



Logging	Trapping	K	Migrants	PE	TE	N	H	R
No logging	No trapping	50	0	100	63	--	--	--
			2	0	--	48	93	0
			20	0	--	50	99	0
		100	0	34	95	15	62	--
			2	0	--	97	94	0
			20	0	--	98	99	0
	Trapping	50	0	100	29	--	--	--
			2	0	--	17	92	0
			20	0	--	48	99	0
		100	0	100	34	--	--	--
			2	0	--	21	93	0
			20	0	--	81	99	0
Logging	No trapping	50	0	100	52	--	--	--
			2	0	--	22	92	0
			20	0	--	25	98	0
		100	0	100	73	--	--	--
			2	0	--	43	93	3
			20	0	--	48	99	3
	Trapping	50	0	100	27	--	--	--
			2	0	--	12	92	5
			20	0	--	25	98	1
		100	0	100	33	--	--	--
			2	0	--	16	92	5
			20	0	--	45	99	2

Fig. 1. Scenarios tested for population vulnerability, and results obtained from 1000 simulations of 100 years for each scenario. Nodes with boxes indicate management decisions; nodes with circles indicate random variables determined by population and habitat structure. See text for descriptions of scenarios. PE = probability of extinction; TE = mean time to extinction; N = mean number of martens in nonextinct populations after 100 years; H = mean percent of initial heterozygosity remaining in extant populations at 100 years; R = number of populations undergoing temporary extinction and recolonization during the 100-year simulation.

sexes (see below), and the delayed breeding by males, the expected ratio of adult (>2 years of age) males to adult (>1 year of age) females is 1:1.76 (obtained from life table analysis). Some adult males (37%) were assumed to be excluded from the breeding population so that, with Poisson distribution of reproductive success, the mean successfully breeding male would sire 3.0 litters. The calculations to determine the necessary proportion of adult males in the breeding pool to yield the desired degree of polygamy, given the age-sex structure of the population and a Poisson distribution [illegible] reproductive success, are done automatically [illegible] VORTEX program.

We assumed 50% first-year mortality (as reported by Strickland et al. 1982), 25% second-year mortality of males, and 10% annual mortality of males older than 2 years and females older than 1 year. We further assumed that martens senesce after their tenth year. Given the mortality schedule, very few (about 0.25%) animals would live beyond 10 years of age, and the assumption of senescence in the model has very little impact on the results obtained.

Lacking any information on the impact of inbreeding on survival of martens, we modeled the effect of inbreeding depression by assuming that inbreeding would depress survival to the extent (3.14 lethal equivalents) reported by Ralls et al. (1988) as the median of 40 mammalian populations. This level of inbreeding depression reduces the survival of the progeny of full-sib matings by about 32%.

The populations studied by Ralls et al. were all captive (in zoos or research labs), provided with unlimited food, and protected from exposure to disease, predation, and inclement weather. The impact of inbreeding on wild populations may be greater if inbreeding reduces an animal's ability to cope with stresses.

Environmental variation in the above demographic parameters was modeled by assuming that the probability of breeding by adult females varies across years according to a binomial distribution with mean 95% (as described above) and standard deviation of 5%. Environmental variation in mortality rates was modeled for each age-sex class by setting the binomial standard deviation at one-fourth the mean (i.e., 50% ± 12.5% first year mortality, 25% ± 6.25% second-year mortality of males, and 10% ± 2.5% annual mortality of adults).

Two types of catastrophes were modeled, each with a probability of occurrence of 1% each year of the simulation. The first type of catastrophe (e.g., disease) was assumed to kill, on average, 30% of the population but to have no effect on reproduction of the survivors. A second type of catastrophe (e.g., fire) was assumed also to kill 30% of the animals but then to reduce reproduction by 10% during that year.

Population size and migration between populations are likely to vary widely among populations, and we tested several possible values (populations of 50 or 100, with exchange of 0, 2, or 20 martens per year) to determine the sensitivity of a population to these parameters. The simulated populations were started at the stable age distribution calculated from the mortality schedule.

Finally, some aspects of the population dynamics are under direct control of resource managers. We examined the impact of trapping (modeled as a harvest of 20% annually) and logging (modeled as a loss of 1% of habitat per year over 50 years) on population viability to help define acceptable levels of human disturbance.

SIMULATION RESULTS

The marten population scenarios listed above were simulated, and results were expressed in terms of probability of extinction (PE), mean time to extinction (T), number of animals (N) remaining at the end of the simulation (in those simulated populations not extinct), mean percent of initial heterozygosity remaining (H), and number of recolonizations (R) out of 1000 simulations (Fig. 1). Each population was simulated for 100 years and was repeated 1000 times for each set of parameters. These results are not sufficient to specify precisely the vulnerability of marten populations to local extinction. Without detailed data on a specific population of interest, such conclusions cannot be obtained with the VORTEX simulation program or by any other technique. The results do, however, illustrate how computer simulation can be used to examine the vulnerability of marten populations under various possible scenarios. The scenarios examined might represent the range of plausible values of population parameters that are poorly known, or various possible management options, or (as illustrated below) both.

Life table analysis using the Leslie matrix approach (Leslie 1945), carried out by the VORTEX program in addition to stochastic modeling, yields a mean expected population growth rate of 29.2% with the basic birth and death parameters specified above, and 3.4% mean population growth under the scenarios with survival reduced by 20% due to trapping. Although mean population growth was initially positive in each scenario modeled (and growth observed in simulated populations closely matched the expected population growth calculated from the life table), genetic and demographic fluctuations resulted in high probability of population extinction in all cases in which the population was isolated from other populations. In the absence of exchange of migrants, only the most optimistic scenario (no trapping, no logging, carrying capacity of 100) had a probability (66%) of surviving 100 years (Fig. 1, line 4). Without immigration and emigration, the genetic variability was rapidly eroded in populations of 50 or 100 martens (Fig. 2a), resulting in steady reduction in viability (inbreeding depression) and eventually population crash to extinction (Fig. 2b). The exchange of just a pair of migrants per year was sufficient to prevent damaging losses of genetic variation (Figs. 3a,b). Exchange of 10 pairs per year (i.e., a population open to regular interchange) prevented

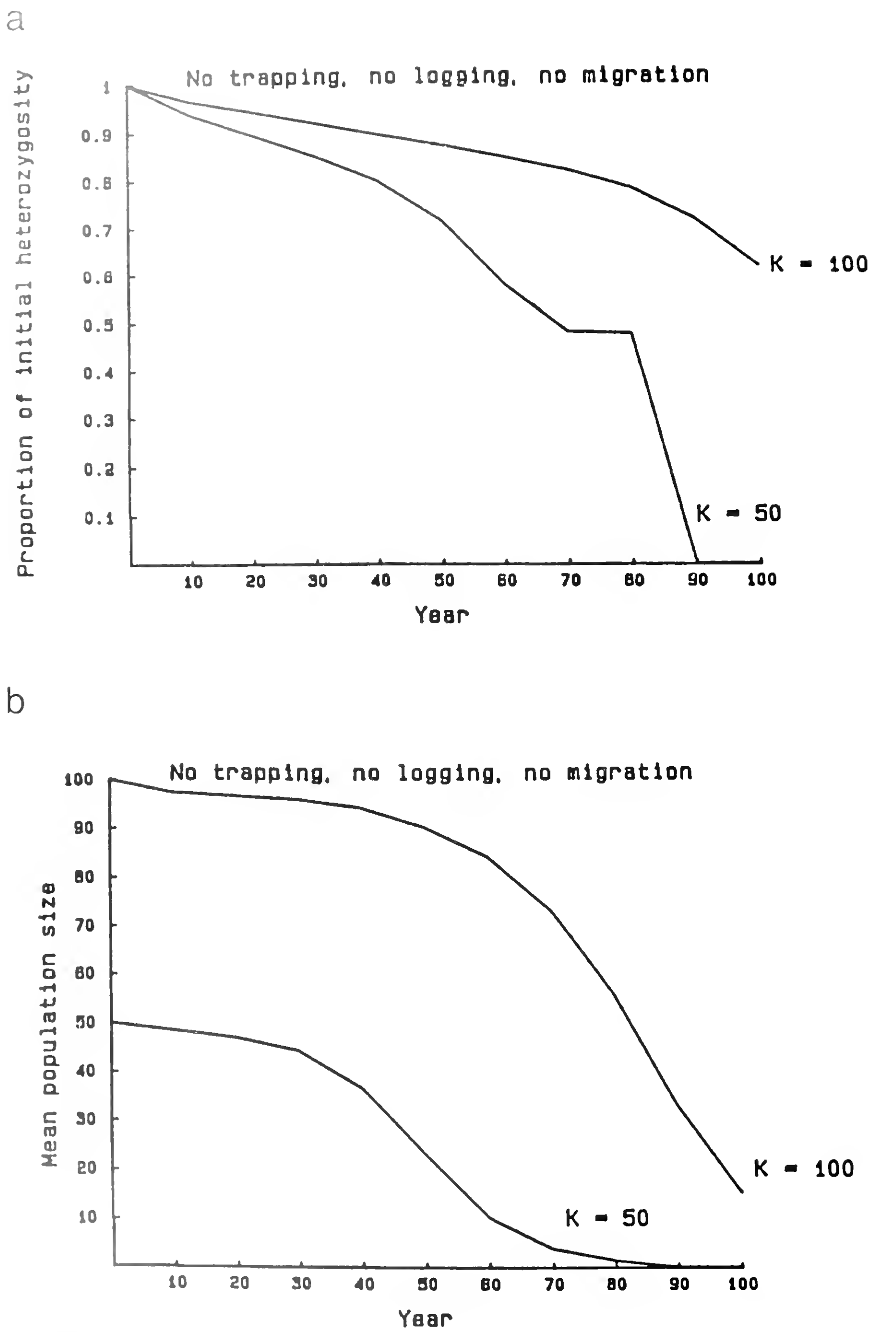


Fig. 2. Fates of 1000 simulated populations with respect to proportion of initial heterozygosity (a) and population size (b) over 100 years. Population parameters modeled as described in text, with no trapping, no logging of habitat, and no immigration or emigration, in habitats with carrying capacity (K) of 50 or 100.

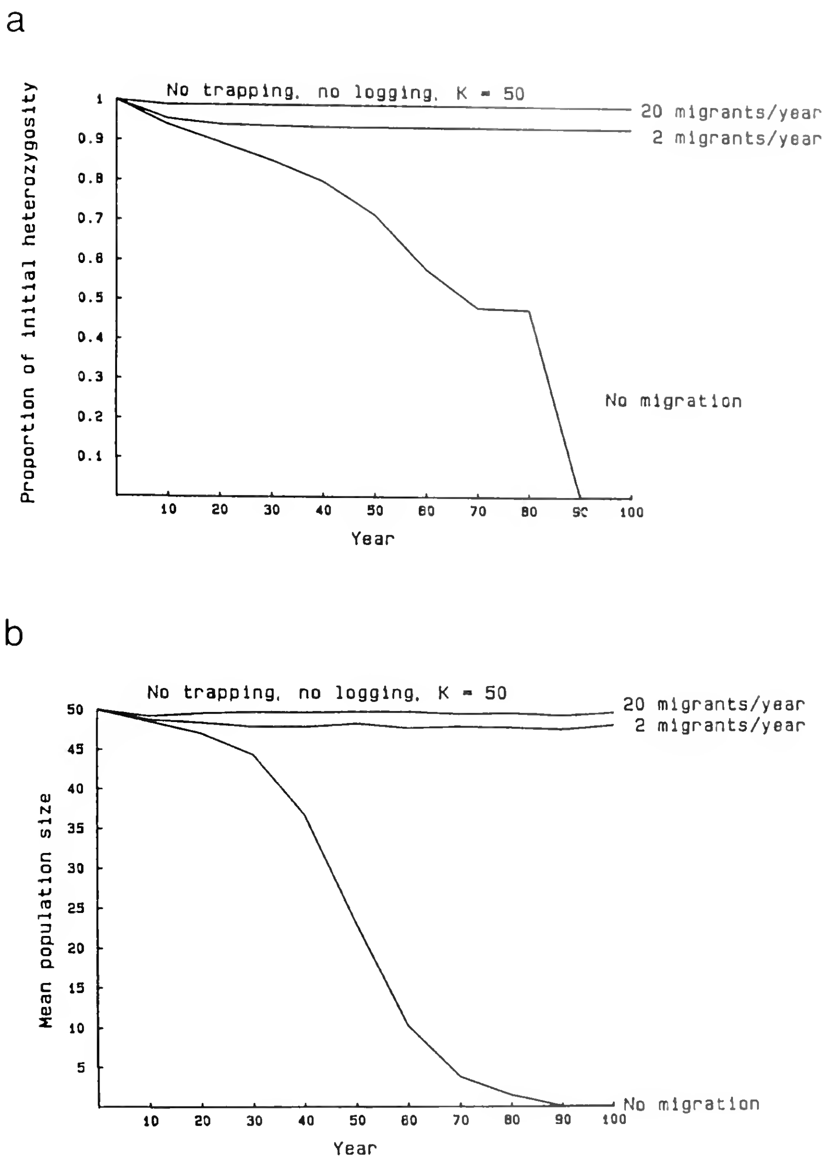


Fig. 3. Fates of 1000 simulated populations with respect to proportion of initial heterozygosity (a) and population size (b) over 100 years. Population parameters modeled as described in text, with no trapping, no logging of habitat carrying capacity of 50, and 0, 2, or 20 migrants exchanged per year.

virtually any loss of genetic variation. In a few of the 1000 simulated populations in each scenario incorporating migration, the modeled populations went temporarily extinct due to random fluctuations in reproduction and mortality, but they were successfully recolonized by immigrants (Fig. 1, last column).

Trapping, removing 20% of each age class annually, accelerated the loss of genetic variation and consequent extinction in closed populations but was sustainable in populations that received continued input of genetic variation via immigration (Figs. 1a,b). Logging, a reduction in 50% of the habitat (and therefore a reduction of 50% in the habitat carrying capacity) over 50 of the 100 years of the simulation, similarly accelerated inbreeding and extinction when there was no migration, but was also sustainable if genetic variation was continually restored via exchange with other

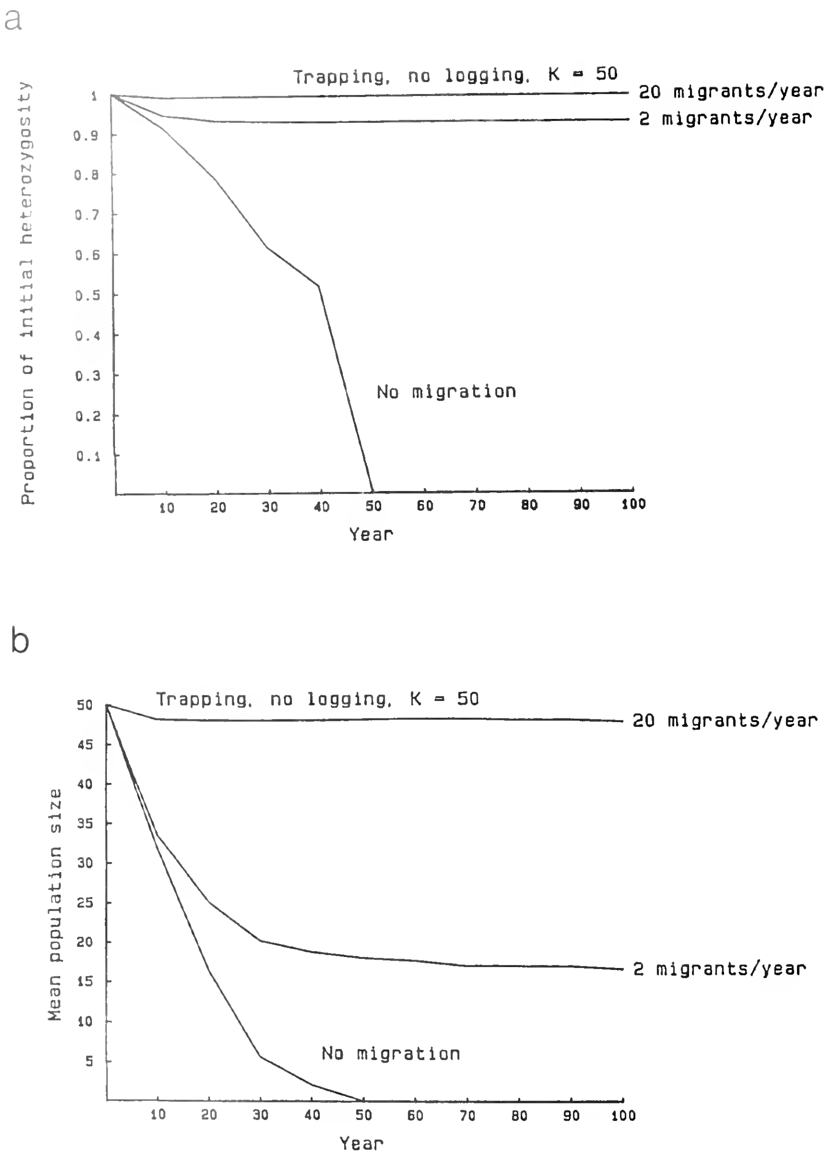


Fig. 1. Fates of 1000 simulated populations with respect to proportion of initial heterozygosity (a) and population size (b) over 100 years. Population parameters modeled as described in text, with survival of each age-sex class reduced 20% by trapping, no logging of habitat, carrying capacity of 50, and 0, 2, or 20 migrants exchanged per year.

populations (Fig. 1, lower half). When immigration was low into trapped and/or logged populations, the effects of inbreeding depressed the mean population sizes below the carrying capacities modeled but did not lead to steady erosion of population viability (see Figs. 1a,b, and compare lines of Fig. 1 with 2 migrants to adjacent lines with 20 migrants).

DISCUSSION

Population modeling is essential to "adaptive management" of martens and other species. Adaptive management uses actual management practices as an experiment to learn from, and modify as needed (Holling 1978). PVA not only permits trends in marten populations under current management to be identified and quantified, but also permits determination of those factors that exert influence on the trends. Modeling population behavior is an important advantage in the conservation and management of populations. There are few, if any, other techniques currently available to synthesize the cumulative impacts of a complex of factors on a population (Lindenmayer et al. 1991). This is important because many recent studies have shown that the dynamics of populations change in relation to their size and context. As a result, PVA is useful in addressing key marten management questions. For example, (1) What is the relationship between population size and population stability? (2) At what population size do random events become important and which of these factors are most critical? (3) What population target will ensure marten population persistence in the management unit? Thus, PVA can be used to model these and other questions and the likely consequences of various management options.

The outcomes of management actions, which must be monitored to permit adaptive management, provide a test of the adequacy of the model and data used to guide the management and provide refined data for improving the accuracy of PVA that will be used to guide future management. As better data and better models become available, PVA modeling should be repeated and reexamined. Used in these ways, PVA can be a key tool in adaptive management and a powerful method for improving and testing our understanding of population biology.

It is important to recognize that, like any model of the natural world, the results of PVA are only as accurate as the data that are fed into the model. Moreover, while PVA allows exploration of the interacting effects of many population processes, any PVA model is still a simplified picture of the real world. Factors that are not modeled or not critically examined might be influencing population dynamics in unknown ways (Lindenmayer et al. in press). Critical management plans should therefore incorporate margins of error appropriate to the uncertainty about the completeness of the models used, the accuracy of the data, and the potential cost of failed management.

PVA is useful in identifying declining marten population trends at an early stage, the essence of adaptive management, thus allowing populations to be managed appropriately before they become highly vulnerable to extinction. PVA can help identify population processes that are likely to endanger a population in the future if corrective management actions (e.g., development of corridors to allow genetic and demographic exchange) are not taken. Management of a species is relatively inexpensive and organizationally simple when multiple healthy populations still exist compared to when the species becomes endangered (Clark et al. 1989 [Designing and managing]).

Results of the marten PVA can be translated into area requirements needed by local populations. For illustration, assume that a manager wants to maintain a marten population, and because of circumstances beyond his control, with no possibility of immigration. The preliminary PVA results in Figures 1 and 2 indicate that well over 100 individuals are needed. If a male and three female marten occupy about 3 km^2, 100 martens would require 75 km^2. PVA results, combined with field studies of home ranges, can be used to determine habitat area needed for wild marten populations. Various combinations of habitat patches and interconnecting corridors can be examined, in part, through PVAs to explore extinction probabilities and management options. Additionally, management options can be further explored by coupling PVA with decision analysis (Maguire et al. 1990). PVA combined with decision analysis, using reliable field data on marten populations, offers the best adaptive management approach currently for this fascinating forest carnivore.

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SUMMER HABITAT USE AND SELECTION BY FEMALE SAGE GROUSE (*CENTROCERCUS UROPHASIANUS*) IN OREGON

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ABSTRACT.—Cover types and vegetative characteristics (e.g., grasses, forbs, shrubs) used by female Sage Grouse (*Centrocercus urophasianus*) during summer were compared with available habitat on two study areas in southeastern Oregon. Broodless hens, which constituted 114 of the 125 (91%) radio-marked hens studied, selected big (*Artemisia tridentata* subspp.) and low sagebrush (*A. arbuscula*) cover types at both study areas. At Hart Mountain, broodless hens did not select specific vegetative characteristics within cover types. However, at Jackass Creek, forb cover was greater ($P = .004$) at broodless hen sites than at random locations. Differences in habitat use by broodless hens between study areas were associated with differences in forb availability. Broodless hens used a greater diversity of cover types than hens with broods. Broodless hens gathered in flocks and remained separate from but near hens with broods during early summer. By early July broodless hens moved to meadows while hens with broods remained in upland habitats.

Key words: Sage Grouse, Centrocercus urophasianus, *Oregon, female, broodless hens, habitat, movements, summer, broods, use, selection.*

Productivity of Sage Grouse (*Centrocercus urophasianus*) is among the lowest of North American grouse (Edminster 1954:130). Reported nest failure ranged from 76% in Oregon (Batterson and Morse 1948) to 36% (Wallestad and Pyrah 1974) in Montana. Consequently, a relatively large percentage of summer Sage Grouse populations consists of broodless hens. However, information on broodless hens is largely anecdotal. Only observations of the proximity of broodless hens to hens with broods (Dalke et al. 1963, Martin 1976) and chronology of summer movements by broodless hens (Petersen 1980, Connelly et al. 1988) have been reported. No study has dealt specifically with habitat use by broodless Sage Grouse.

We investigated habitat use by broodless hens on a hierarchical order of selection (Johnson 1980). We hypothesized that broodless Sage Grouse selected cover types (third-order selection) and vegetative characteristics within cover types (fourth-order selection) and that selection differed between broodless hens and hens with broods. Our objectives were to identify cover types used by broodless hens in relation to availability, to identify vegetative characteristics at broodless hen sites and compare those to randomly selected locations, and to assess habitat use by broodless hens in relation to hens with broods on two study areas.

STUDY AREAS

The study areas were located in southeastern Oregon at Hart Mountain National Antelope Refuge (Lake County) and at Jackass Creek (Harney County). Topography at both areas consists of flat sagebrush plains interrupted by rolling hills, ridges, and draws. Elevations range from 1500 to 2450 m at Hart Mountain and from 1200 to 1700 m at Jackass Creek. Vegetation at both areas is dominated by low sagebrush (*Artemisia arbuscula*), big sagebrush (*A. tridentata vaseyana*, *A. t. wyomingensis*, and *A. t. tridentata*), green rabbitbrush (*Chrysothamnus viscidiflorus*), and western juniper (*Juniperus occidentalis*). Stands of curl-leaf mountain-mahogany (*Cercocarpus ledifolius*) and quaking aspen (*Populus tremuloides*) occur only at Hart Mountain. Common annual and perennial forbs include mountain-dandelion (*Agoseris* spp.), milkvetch (*Astragalus* spp.), hawksbeard (*Crepis* spp.), lupine (*Lupinus* spp.), and phlox (*Phlox* spp.). Grasses consist largely of bluegrass (*Poa* spp.), bluebunch wheatgrass (*Agropyron*

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spicatum), needlegrass (*Stipa* spp.), fescue (*Festuca* spp.), giant wildrye (*Elymus cinereus*), and bottlebrush squirreltail (*Sitanion hystrix*). Plant nomenclature from Hitchcock and Cronquist (1987) was used.

METHODS

Female Sage Grouse were captured (Giesen et al. 1982) during summer 1988, spring and summer 1989–90, and spring 1991. Each hen was fitted with a numbered aluminum leg band and a poncho-mounted, solar-powered radio transmitter with a nickel-cadmium battery (Amstrup 1980). Radio-marked hens were monitored during summer (June–August) 1989–91 at an average rate of no more than twice monthly to minimize the problem associated with lack of independence of locations. Furthermore, we recaptured and removed radios from hens at the conclusion of each field season, and previously unmarked hens were fitted with radios for use in subsequent years to maintain independence of samples among years. Nevertheless, we acknowledge there may be a potential bias in the use of re-observations, even at a low rate of frequency, of the same individuals within a breeding season.

All locations of radio-marked hens were mapped as Universal Transverse Mercator coordinates. Visual locations of radio-marked broodless hens were marked and served as sites for vegetation sampling during June and July 1990. Date, location, and flock size of broodless hens and hens with broods observed on each study area were recorded. Definitions of monthly time periods were early (first 10 days), mid (middle 10 days), and late (last 10 days).

Eleven cover types were defined on the basis of dominant shrubs and grasses (Gregg 1992). We used color infrared aerial photographs and topographic maps to delineate cover types on each study area. Each hen location was classified into 1 of the 11 cover types. At each study area available habitat was determined with the minimum convex polygon method (Odum and Kuenzler 1955) from telemetry locations obtained during summer. Proportions of cover types within the available habitat at each area were determined with a dot grid system (Avery 1977).

We characterized vegetation at sites used by broodless hens within two days after visual locations were determined. Canopy cover (%) of shrubs was measured by line intercept (Canfield 1941) along two 10-m perpendicular transects intersecting at the broodless hen site. The position of the first transect was determined from a randomly selected compass bearing. Each shrub intercepted was placed into one of three height classes: short (<40 cm), medium (40–80 cm), or tall (>80 cm). Canopy cover of shrubs was recorded separately for each height class. Cover (%) of forbs and grasses was estimated in five 20 × 50-cm plots equidistantly spaced along each transect (Daubenmire 1959). Vegetation was characterized at randomly located points during June and July with the same methods used to measure variables at broodless hen sites. Random sites were located with a random numbers table, which was used to determine starting point, compass bearing, and distance traveled.

We compared the use of cover types by broodless hens with availability of cover types within study areas from June through August. The proportions of cover types available were used to establish the expected values for frequency of bird observations occurring in those cover types. We also compared cover type use between broodless hens and hens with broods. Chi-square analysis was used for these tests. Cover types with expected values of <5 bird observations were combined and analyzed collectively. If differences were detected, confidence intervals were calculated to identify cover types that contributed to the difference (Neu et al. 1974, Byers et al. 1984).

We used a factorial analysis of variance (ANOVA) (PROC GLM, SAS Institute, Inc. 1989) to compare vegetative characteristics among plot types (broodless hen or random). Study area was an additional factor in the ANOVA model to account for variation associated with spatial differences (Snedecor and Cochran 1967:339). A significant plot type (hen use site or random location) × study area interaction ($P = .02$) was detected for forb cover. Consequently, differences among plot types for forb cover were reported by study area. A single-factor ANOVA was used to compare vegetative characteristics at random locations between study areas in cover types used by broodless hens. We assumed our data

TABLE 1. Use (%) of cover types during summer (June–August) by radio-marked broodless Sage Grouse hens at Hart Mountain National Antelope Refuge ($n = 67$ hens, 168 locations) and Jackass Creek ($n = 47$ hens, 137 locations) study areas, Lake and Harney counties, Oregon, 1989–91.

	Hart Mountain			Jackass Creek		
Cover type	% avail	% use	X^2	% avail	% use	X^2
Low sagebrush/bunchgrass	14	30	7.1	37	18	14.0
Wyoming big sagebrush	0	0		11	36	0.9
Mountain big sagebrush	20	34	16.3	0	0	
Mixed sagebrush	0	0		11	39	95.5
Grassland	12	8	1.9	0	0	
Low sagebrush/fescue	5	15	36.9*	0	0	
Meadow	3	10	23.8	0	0	
Other[a]	16	2	19.5	11	8	1.1

[a]Includes basin big sagebrush, lakebed, and mountain shrub.

*Use differed ($P < .05$) from availability.

were normally distributed (PROC UNIVARIATE, SAS Institute, Inc. 1989), and we considered our results significant if $P \leq .05$.

RESULTS

One hundred fourteen radio-marked broodless hens (67 at Hart Mountain and 47 at Jackass Creek) were relocated 305 times (168 locations at Hart Mountain and 137 locations at Jackass Creek). Seven radio-marked hens with broods at Hart Mountain were relocated 90 times, and 4 radio-marked hens at Jackass Creek were relocated 55 times during the same time period. Available habitat encompassed 393 km^2 at Hart Mountain and 563 km^2 at Jackass Creek. Vegetative characteristics were measured at 112 broodless hen sites (22 and 90 at Hart Mountain and Jackass Creek, respectively) and 100 random locations (30 at Hart Mountain and 70 at Jackass Creek).

Small flocks of broodless hens (2–3 birds) were first observed during mid-May at both study areas. By early June, flocks of as many as 25 broodless hens were commonly found in low sagebrush, big sagebrush, and mixed sagebrush (mosaic of low and big sagebrush) cover types. Broodless hens remained near hens with broods until early July and then moved to meadows. Numbers of broodless hens in meadows increased until by late July flocks of >100, which potentially may have contained some early hatched young birds, were observed. Typically, however, hens with broods remained in sagebrush upland habitats until early August and then moved to meadows and joined broodless hens.

Broodless hens used mountain big sagebrush, low sagebrush/fescue, and meadow habitats at Hart Mountain and mixed sagebrush at Jackass Creek more frequently ($P < .05$) than expected, based on availability (Table 1). Low sagebrush bunchgrass was used less frequently ($P < .05$) than expected at both study areas (Table 1). Cover-type use differed ($P < .05$) between broodless hens and hens with broods. Broodless hens used less low sagebrush/fescue and more low sagebrush/bunchgrass, grassland, and meadow than hens with broods at Hart Mountain and used more mixed sagebrush than hens with broods at Jackass Creek (Table 2).

At Jackass Creek forb cover (%) was greater ($P = .004$) at broodless hen sites ($\bar{x} = 4$, SD $= 4$, $n = 90$) than at random locations ($\bar{x} = 2$, SD $= 3$, $n = 70$). However, at Hart Mountain forb cover did not differ ($P = .37$) between broodless hen ($\bar{x} = 10$, SD $= 6$, $n = 22$) and random ($\bar{x} = 12$, SD $= 9$, $n = 30$) sites. No differences ($P > .05$) in other habitat characteristics were detected between broodless hen and random locations (Table 3). Cover of forbs, grasses, and short shrubs was greater and tall shrubs was less ($P < .05$) in cover types used at Hart Mountain than at Jackass Creek (Table 4). Differences in canopy cover of short and tall shrubs between study areas reflected cover types used by broodless hens at the two areas. Canopy cover of all height classes of shrubs combined was similar between areas (26% and 25% at Hart Mountain and Jackass Creek, respectively).

DISCUSSION

Differences in habitat use by broodless hens between study areas were attributed to differences in forb availability. Forbs are an

TABLE 2. Use (%) of cover types during summer (June–August) by radio-marked female Sage Grouse at Hart Mountain National Antelope Refuge and Jackass Creek study areas, Lake and Harney counties, Oregon, 1989–91.

	Hart Mountain			Jackass Creek		
Cover type	Broodless (67/168)[a]	Brood (7/94)	X^2	Broodless (47/137)	Brood (4/55)	X^2
Low sagebrush bunchgrass	30*	6	151.3*	18	24	2.2
Wyoming big sagebrush	0	0		36	42	1.2
Mountain big sagebrush	34	40	1.75	0	0	
Mixed sagebrush	0	0		39*	22	17.9*
Grassland	8*	1	84.5*	0	0	
Low sagebrush fescue	15*	49	38.4*	0	0	
Meadow	10*	3	21.1*	0	0	
Other[b]	2	0		8	13	2.4

[a] Sample size indicated by numbers within parentheses (number of hens/number of locations).

[b] Includes basin big sagebrush, lakebed, and mountain shrub.

*Use differed ($P < .05$) between broodless hens and hens with broods.

TABLE 3. Vegetative characteristics (% cover) at sites used by radio-marked broodless Sage Grouse hens and random locations at Hart Mountain National Antelope Refuge and Jackass Creek study areas, Lake and Harney counties, Oregon, June and July 1990.

		Broodless hen sites (n = 112)		Random sites (n = 100)	
Characteristic	P value	$\bar{x}$	SD	$\bar{x}$	SD
Forb cover[a]		5	5	5	7
Grass cover	.06	10	9	9	6
Shrub cover					
Short, <40 cm	.69	14	10	14	10
Medium, 40–80 cm	.16	11	8	8	9
Tall, >80 cm	.59	4	6	3	5

[a] Because of significant plot type × forb cover interaction ($P = .02$), forb cover was tested individually by study area. Forb cover was greater ($P > .05$) at broodless hen sites than at random locations at Jackass Creek but not at Hart Mountain.

important component of the diet of hens during summer (Patterson 1952:203, Wallestad et al. 1975). In Montana, Sage Grouse shifted from a diet of sagebrush to forbs in summer (Wallestad 1975). The change was attributed to availability and palatability of forbs. In cover types used at Hart Mountain, forb availability was relatively high, and broodless hens did not use sites within cover types on the basis of forb availability. These cover types (mountain big sagebrush, low sagebrush/fescue, meadow) were available at higher elevations (>1800 m) and presumably received greater amounts of precipitation, which may have increased forb production and delayed forb phenology compared with low-elevation sites. However, at Jackass Creek, where forb availability was low, sites used by broodless hens had greater forb cover than did random locations.

Big and low sagebrush cover types were used by broodless hens at both study areas. Broodless hens in Nevada used open areas of low sagebrush for feeding and dense clumps or patches of big sagebrush for roosting (Klebenow 1972). In Montana, flocks of broodless hens were typically found in areas of dense sagebrush throughout summer (Wallestad 1975). Schoenberg (1982) reported that broodless hen sites in Colorado had greater sagebrush cover than did random locations. Our findings, however, indicated broodless hens did not select sites based on canopy cover of shrubs.

Our study revealed differences in chronology of summer movements and cover types used between broodless hens and hens with broods. Broodless hens gathered in flocks and remained separate from but in the vicinity of hens with broods during early summer. However, broodless hens moved to meadows earlier in summer and used a greater diversity of cover types than hens with broods. Several authors reported similar behavior and

TABLE 4. Vegetative characteristics (% cover) at random locations at Hart Mountain National Antelope Refuge and Jackass Creek study areas, Lake and Harney counties, Oregon, June and July 1990.

		Hart Mountain (n = 30)		Jackass Creek (n = 70)	
Characteristic	P value	$\bar{x}$	SD	$\bar{x}$	SD
Forb cover	.0001	12	9	2	[illegible]
Grass cover	.0001	13	9	7	[illegible]
Shrub cover					
Short, <40 cm	.0008	19	10	12	10
Medium, 40–80 cm	.25	6	12	9	8
Tall, >80 cm	.0006	1	1	1	6

chronology of summer movements by broodless hens (Batterson and Morse 1948, Dalke et al. 1963, Martin 1976, Connelly et al. 1988). Petersen (1980) reported that the early movement to meadows by broodless hens was related to nest loss and not desiccation of vegetation in uplands. Contrastingly, Schoenberg (1982) noted that summer movements by broodless hens and hens with broods occurred simultaneously and were probably a response to vegetation desiccation in sagebrush uplands.

Differences in summer habitat use between broodless hens and hens with broods may be attributed to specific dietary requirements of juvenile Sage Grouse. Juvenile Sage Grouse consume primarily forbs and insects during summer (Rasmussen and Griner 1938, Patterson 1952:201, Peterson 1970). Johnson and Boyce (1990) demonstrated that survival and growth of captive Sage Grouse chicks decreased as the quantity of insects in the diet decreased. Furthermore, hens with broods selected areas with less sagebrush (Klebenow 1969, Dunn and Braun 1986) and greater availability of forbs (Klebenow 1969, Peterson 1970, Wallestad 1971). Presumably, hens with broods remained in uplands until succulent forbs were no longer available; they then moved to meadows later in summer (Petersen 1980). Dietary needs of broodless hens might be less specific than those of hens with broods; as a consequence, broodless hens moved from uplands to meadows earlier in summer and used a greater diversity of cover types than hens with broods.

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PREY SELECTION AND FOOD HABITS OF BURROWING OWLS IN COLORADO

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ABSTRACT.—Food habits of Burrowing Owls (*Speotyto cunicularia*) were studied during the breeding seasons of 1990 and 1991 in central Colorado. Concurrent insect availability studies were conducted to determine selection for specific insect families. Analysis of 1145 castings indicated use of only one insect family, the carrion beetles (Silphidae), at a rate greater than expected based on availability in one year. Castings and prey remains showed different dietary components. Prey remains showed greater use of small mammals, moths, amphibians, and passerines, and castings indicated greater use of mice and beetles. Methodology in raptor food habits studies may therefore bias results.

Key words: Speotyto cunicularia, *Burrowing Owl, food habits, casting, prey remains, Colorado.*

Much of the diet literature for Burrowing Owls (*Speotyto cunicularia*) consists solely of studies based on casting analysis. Study of Burrowing Owl food habits based on prey remains found near burrows has shown prey items not detected from casting analysis (Thomsen 1971, MacCracken et al. 1985). Most food habits studies lack concurrent quantitative studies of prey populations. This deficiency is also apparent in raptor food habits studies (Brown 1974, Olendorff and Stoddart 1974).

In 1987 the Rocky Mountain Arsenal (RMA) was established as an Environmental Protection Agency superfund site, and cleanup operations were initiated. Cleanup of RMA may require alterations to existing habitats, possibly affecting the Burrowing Owl prey base. The primary objective of this study was to determine the food habits of Burrowing Owls nesting at RMA, and how use of insects by Burrowing Owls is related to availability. This will allow a better understanding of the effects of environmental cleanup at RMA on Burrowing Owls. Our second objective was to investigate potential differences in diet from analyses of castings and prey remains.

STUDY AREA

RMA is located in south central Adams County, Colorado, and encompasses 6900 ha. As part of the High Plains district of the Northern Great Plains province in the North Temperate Grassland Biome, RMA has a semiarid climate and features low humidity, light rainfall, and moderate to high winds. Average annual precipitation is about 38 cm. Elevation ranges from 1564 m to 1625 m above sea level (Environmental Science and Engineering 1989).

Vegetation is represented by five major communities: weedy forbs, cheatgrass (*Bromus* spp.)/weedy forbs, cheatgrass/perennial grassland, native perennial grassland, and crested wheatgrass (*Agropyron cristatum*). Minor communities include sand sagebrush (*Artemisia filifolia*) shrubland, rubber rabbitbrush (*Chrysothamnus nauseosus*) shrubland, yucca (*Yucca* spp.) grassland, cottonwood (*Populus deltoides*), and willow (*Salix* spp.) (Environmental Science and Engineering 1989).

MATERIALS AND METHODS

Food Habits

Food habits were studied by analysis of regurgitated castings and prey remains. Castings were collected and prey remains recorded at burrows biweekly from 14 June to 9 August 1990 ($n = 19$ burrows) and from 5 April to 26 July 1991 ($n = 28$ burrows). Castings were separated by date of collection and by burrow. Castings were soaked overnight in a 2 molar (8%) NaOH solution, leaving only bone and chitin (Degn 1978). Contents were

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separated and enumerated to the lowest possible taxon, usually family. Burrowing owls normally consumed only a portion of many prey items. For this reason, the percentage of a given prey item in the diet was based on frequency of occurrence, rather than an estimate of percent biomass.

Data were tested within years for among-burrows variation in use of each insect family found in castings. Wilcoxon ranked-sum tests were used (SAS Institute, Inc. 1988).

Insect Use and Availability

Pitfall traps were used to determine relative abundances of insects near occupied burrows (Wolda 1990). Traps consisted of six 10-oz clear plastic cups buried flush with the soil surface, placed at 1-m intervals from all burrows ($n = 47$) in a randomly selected azimuth. This ensured that insect sampling occurred in the birds' foraging microhabitat (Hutto 1990). Traps were set for one week and were filled to a depth of about 4 cm with a 25% solution of ethylene glycol to act as a preservative. Two trapping intervals were used, separated by one month.

Data were tested for differences between trapping intervals and years using Kruskal-Wallis and Wilcoxon 2-sample tests (SAS Institute, Inc. 1988). No differences ($P < .05$) were detected between trapping intervals, so data were pooled. A year effect ($P < .05$) was detected for both insect use and availability, so data were analyzed by year. A X^2 goodness-of-fit test was used to test for overall differences in use and availability. When significant differences were detected, Bonferroni confidence intervals were used to identify differences within individual insect family classes (Neu et al. 1974, Byers et al. 1984).

Castings Versus Prey Remains

Frequency of occurrence of prey items in castings and as prey remains was tested for between-year differences. Yearly differences and differences in contents of castings and prey remains were tested using Kruskal-Wallis and Wilcoxon 2-sample tests (SAS Institute, Inc. 1988).

RESULTS

Diets

In 19[illegible] castings contained 759 prey [illegible] families in 4 orders. In 1991, 680 castings contained 944 prey individuals from 9 families in 3 orders. Invertebrates made up 48.4% of diets in 1990, and 61.2% in 1991 based on casting analysis (Table 1). Prey remains for 1990 and 1991 included 187 individuals from 18 families in 6 orders (Table 2).

Use of only tiger beetles (Cicindelidae) differed ($P = .001$) among burrows in 1990. No differences ($P > .05$) were found among burrows in 1991.

Insect Use and Availability

In 1990, 705 insects from 10 families were captured in pitfall traps, and 7 families were represented in castings, including 1 family not captured in pitfall traps. The X^2 test indicated a difference between owl use of insects and pitfall-trapped insects ($X^2 = 11{,}963$, $P < .0001$, 10 df), implying that Burrowing Owls selected insect families disproportionately to numbers captured in pitfall traps. Specifically, differences ($P < .05$) were found in use of short-horned grasshoppers (Acrididae), ground beetles (Carabidae), camel crickets (Gryllacrididae), and carrion beetles (Silphidae) in 1990 (Table 3).

In 1991, 4692 insects from 13 families were captured in pitfall traps, and 7 families were represented in castings. As in 1990, the X^2 test indicated a difference between owl use of insects and pitfall-trapped insects ($X^2 = 643$, $P < .0001$, 12 df), but we found no differences ($P > .05$) in use of specific insect families (Table 4). Although more than 20% of categories contained less than five expected observations (Dixon and Massey 1969:238), the average expected observation was well over six for all categories, which made the use of this approximation appropriate (Roscoe and Byars 1971).

Castings Versus Prey Remains

Differences were detected in castings and prey remains for both 1990 and 1991. During both years combined, spadefoot toads (Salientia) and thirteen-lined ground squirrels (*Spermophilus tridecemlineatus*) occurred exclusively ($P < .05$) as prey remains, as did all moths (Lepidoptera) ($P < .0001$). Passerine remains were found once in castings, but more often ($P < .0001$) as prey remains in both years. During 1990 black-tailed prairie dog (*Cynomys ludovicianus*) occurred exclusively

TABLE 1. Frequency and percent occurrence of prey items in castings of Burrowing Owls at the Rocky Mountain Arsenal, Colorado, 1990–91.

	1990		1991		[illegible]	
Prey item	N	%N	N	%N	N	[illegible]
Vertebrates						
RODENTIA						
Cricetidae						
Cryptotis parva	1	0.1	0	0.0	[illegible]	[illegible]
Microtus ochrogaster	40	5.3	66	6.9	106	[illegible]
Peromyscus maniculatus	272	35.8	192	20.3	[illegible]	[illegible]
Passeriformes	1	0.1	0	0.0	[illegible]	[illegible]
Subtotal	314	41.4	258	27.2	[illegible]	[illegible]
Invertebrates						
COLEOPTERA						
Carabidae	1	0.1	20	2.1	21	[illegible]
Cicindelidae	54	7.1	41	4.3	95	[illegible]
Scarabeidae	55	7.2	80	8.5	[illegible]	[illegible]
Silphidae	109	14.3	124	13.1	[illegible]	[illegible]
Tenebrionidae	84	11.1	275	28.9	[illegible]	[illegible]
ORTHOPTERA						
Acrididae	63	8.3	36	3.8	[illegible]	5.8
Gryllacrididae	2	0.3	5	0.5	7	[illegible]
Subtotal	368	48.4	579	61.2	947	[illegible]
Other						
Rocks	52	6.8	104	11.0	156	[illegible]
Glass	1	0.1	0	0.0	1	[illegible]
Vegetation	17	2.2	1	0.1	18	1.0
Eggshell	7	0.9	2	0.2	9	[illegible]
Subtotal	77	10.1	107	11.3	184	[illegible]
Total	759	99.9	941	99.7	[illegible]	[illegible]

[a]tr = <0.1%

as prey remains ($P < .005$), while darkling (Tenebrionidae), scarab (Scarabeidae), and tiger beetles occurred exclusively in castings ($P < .05$). Carrion beetles occurred in castings and prey remains, but in greater numbers ($P < .005$) in castings. During 1991, Ord's kangaroo rat (*Dipodomys ordii*) was recorded exclusively as prey remains ($P < .05$). Short-horned grasshoppers occurred in castings and prey remains, but to a greater extent ($P < .0001$) as prey remains. Deer mice also occurred in both, but to a greater extent ($P < .001$) in castings.

DISCUSSION

Food Habits

While Burrowing Owls took large numbers of several families of Coleopterans, we believe that these prey items were taken opportunistically by day and mammalian prey were hunted exclusively at night. Haug and Oliphant (1990) never observed Burrowing Owls foraging diurnally for mammals. Likewise, in over 200 hours of observation, mammalian prey deliveries to the burrow during daylight were witnessed only twice at RMA in 1990 and 1991 (Plumpton 1992). Use of insect families varied little between nesting burrows. Both castings and prey remains revealed that deer mice were the single most important prey species on this site.

Insect Use and Availability

Burrowing Owls at RMA took insects in the families Acrididae, Carabidae, and Gryllacrididae at a rate less than expected, while preying on the family Silphidae more than expected based on pitfall trap results in 1990. In 1991 Burrowing Owls preyed on insect [illegible] of Burrowing Owls based on prey remains found during biweekly searches at the Rocky Mountain Arsenal [illegible] 1990 and 5 April–26 July 1991.

Prey	1990		1991		Total	
	N	%N	N	%N	N	%N
Vertebrates						
RODENTIA						
Cricetidae						
Microtus ochrogaster			11	8.5	11	5.9
Peromyscus maniculatus	40	67.8	10	7.8	50	26.7
Sciuridae						
Cynomys ludovicianus	1	1.7			1	0.5
Spermophilus tridecemlineatus	1	1.7	1	0.8	2	1.1
Heteromyidae						
Dipodomys ordii			1	0.8	1	0.5
PASSERIFORMES						
Alaudidae						
Eremophila alpestris	4	6.8	5	3.9	9	4.8
Emberizidae						
Sturnella neglecta	3	5.1	3	2.3	6	3.2
Icterus galbula			1	0.8	1	0.5
Muscicapidae						
Catharus spp.			1	0.8	1	0.5
Unknown spp.	1	1.7	8	6.2	9	4.8
SQUAMATA						
Viperidae						
Crotalus viridis			1	0.8	1	0.5
SALIENTIA						
Scaphiopus spp.	1	1.7	2	1.5	3	1.6
Subtotal	51	86.5	44	34.2	95	50.6
Invertebrates						
COLEOPTERA						
Carabidae			1	0.8	1	0.5
Cicindelidae			2	1.5	2	1.1
Scarabeidae			2	1.5	2	1.1
Silphidae	2	3.3	8	6.3	10	5.3
Tenebrionidae	2	3.3	25	19.5	27	14.4
LEPIDOPTERA						
Citheroniidae						
Hyalophora cecropia			1	0.8	1	0.5
Saturniidae						
Antheraea polyphemus	1	1.7			1	0.5
Sphingidae						
Celerio lineata			8	6.3	8	4.3
Noctuidae	2	3.3	3	2.3	5	2.7
ORTHOPTERA						
Acrididae	1	1.7	34	26.6	35	18.7
Subtotal	8	13.3	84	65.6	92	49.2
Total	59	99.8	128	99.8	187	99.7

[illegible] pitfall trap results.

[illegible] Remains

Castings [illegible] of deer mice and beetles. Coleo[illegible] remains indicated greater us[illegible] than deer mice, toads, an[illegible] which bones may not have been ingested. We suspected that larger items, such as prairie dog and prairie rattlesnake (*Crotalus viridis*), were scavenged from roadsides. Other authors have recorded organisms from prey remains that were not evident from castings (Thomsen 1971, MacCracken et al. 1985). Recording prey remains while collecting castings

TABLE 3. Use of insect prey by Burrowing Owls at the Rocky Mountain Arsenal, Colorado, 1990.

Insect family	Observed proportion in castings	Expected proportion in castings	Bonferroni interval on proportion
Acrididae	.171	.255	.117 ≤ P ≤ [illegible]
Carabidae	.002	.101	.005 ≤ P ≤ [illegible]
Cicindelidae	.147	0	.094 ≤ P ≤ .199
Coccinelidae	.0	.001	0 ≤ P ≤ 0
Curculionidae	.0	.005	0 ≤ P ≤ 0
Elateridae	.0	.001	0 ≤ P ≤ 0
Gryllacrididae	.005	.167	.005 ≤ P ≤ .016
Lygaeidae	.0	.001	0 ≤ P ≤ 0
Scarabeidae	.149	.078	.096 ≤ P ≤ .202
Silphidae	.296	.004	.228 ≤ P ≤ .364
Tenebrionidae	.228	.101	.165 ≤ P ≤ .291

aSignificant at $P < .05$

TABLE 4. Use of insect prey by Burrowing Owls at the Rocky Mountain Arsenal, Colorado, 1991.

Insect family	Observed proportion in castings	Expected proportion in castings	Bonferroni interval on proportion
Acrididae	.062	.176	.130 ≤ P ≤ .222
Carabidae	.034	.092	.057 ≤ P ≤ .127
Cicindelidae	.071	.075	.044 ≤ P ≤ .108
Cerambycidae	.000	.001	.001 ≤ P ≤ .002
Coccinelidae	.000	.001	−.003 ≤ P ≤ .001
Curculionidae	.000	.001	−.003 ≤ P ≤ .005
Elateridae	.000	.003	−.004 ≤ P ≤ .010
Gryllacrididae	.008	.021	.004 ≤ P ≤ .039
Lygaeidae	.000	.014	.010 ≤ P ≤ .029
Mantidae	.000	.001	.001 ≤ P ≤ .002
Scarabeidae	.138	.371	.313 ≤ P ≤ .429
Silphidae	.214	.089	.055 ≤ P ≤ .124
Tenebrionidae	.471	.154	.110 ≤ P ≤ .197

requires little additional effort and may reveal use of prey items beyond those found in castings.

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TEMPORAL VARIATION IN THE DIETS OF CALIFORNIA QUAIL IN WESTERN OREGON

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ABSTRACT.—This study was designed to describe dietary changes by comparison of information on long-term diet and plant food availability of California Quail (*Callipepla californica*) in western Oregon. We examined crops from 222 California Quail collected in 1976–78 and 1985–87. Diets included 14 key plant foods (annual frequency >15%) among 53 taxa consumed; 10 of the 14 key foods were similar between time periods. Collectively, key foods contributed 87% of the diet by aggregate dry mass during 1985–87; six species of legumes (family Leguminosae) composed 67% of diet. Relative rankings of availabilities of key foods were similar between 1976–78 and 1985–87. This study revealed that quail were opportunistic within the group of key foods because 9 of the 14 key foods were consumed in different frequencies between the two periods. Legumes were an important dietary component in western Oregon because they composed the bulk of the diet, were among the most frequently consumed, and most were taken in substantially greater proportions than available.

Key words. *California Quail,* Callipepla californica, *diet, western Oregon.*

Availability of food influences diet, may cause fluctuations in population levels, and is a key element in sustaining populations of California Quail (Sumner 1935, Emlen and Glading 1945, Leopold 1977:170). Browning (in Leopold 1977:229) summarized diet studies of California Quail from California and noted that a variety of annual plants, particularly filarees (*Erodium* spp.), legumes, and grasses (family Gramineae), furnished the bulk of the diet. In northwestern Oregon (an extended range), several species of legumes, Cichorieae (milky-juiced composites), sorrel (*Rumex* spp.), and bittercress (*Cardamine* spp.) were important foods (Oates and Crawford 1983). Gullion (1966) stated that year-round, long-term diet information, including population status, was critical to understanding habitat management and population dynamics of game birds but was largely lacking from the literature. Additionally, few comparative studies of long-term variations in diet and selection, especially on quail of the western United States, have been performed. Our objectives were to determine annual and seasonal foods of California Quail by frequency and mass during 1985–87 to compare with the frequency of occurrence in crops (use) of key plant foods in 1976–78. Additionally, we compared the annual and seasonal relative availability of plant foods between 1976–78 and 1985–87.

STUDY AREA

The study was conducted on the 650-ha E. E. Wilson Wildlife Area (WWA), 16 km north of Corvallis, Benton County, Oregon. Grasses (predominantly *Festuca* spp.), interspersed with blackberries (*Rubus* spp.), Scot's broom (*Cytisus scoparius*), roses (*Rosa* spp.), and small stands of Oregon white oak (*Quercus garryana*), Oregon ash (*Fraxinus latifolia*), black cottonwood (*Populus trichocarpa*), hawthorn (*Crataegus* spp.), and apple (*Pyrus malus*), characterize the dominant vegetation. Common forbs include vetch (*Vicia* spp.), wild carrot (*Daucus carota*), and teasel (*Dipsacus sylvestris*). Plant nomenclature follows Hitchcock and Cronquist (1973). Annual rainfall averaged 106 cm from 1976 to 1987.

METHODS

Diet was determined from 117 California Quail collected seasonally from fall 1976 to fall 1978 and from 105 California Quail collected seasonally from fall 1985 to fall 1987. Seasons were defined as fall, Sep–Nov; winter, Dec–Feb; spring, Mar–May; and summer

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Jun- Aug. Crops were removed and frozen; frequency of occurrence was determined from sorted crop contents. To address changes in the diet between the two time periods, we compared (1) key plant foods consumed, (2) plant parts taken by the birds, and (3) frequency of occurrence in the diet. Aggregate percent dry mass was calculated for each food item from birds taken in 1985–87 after drying for 24 hours in a 50° C oven. Only frequency data were compared between diets in 1976–78 and 1985–87 because no estimate of mass was made in 1976–78. We defined key foods of California Quail as items occurring at an annual frequency >15% during either 1976–78 or 1985–87. Preliminary analyses revealed that only those foods with an annual frequency >15% constituted ≥ 1% of the diet by mass (1985–87). Although invertebrates were found in 51% of all crops, they composed only 0.5% of diet by mass (Blakely et al. 1988). Chi-square analysis was used to test for seasonal and annual differences in use (frequency of occurrence in crops) of key foods between 1976–78 and 1985–87.

Concurrent with quail collections, we measured availability of vegetation seasonally during fall 1976 to spring 1978 and winter 1985 to fall 1987. To ensure representative sampling, 20 random vegetation transects were placed seasonally throughout WWA in shrub-grassland areas, the only habitat in which foraging quail were observed and where birds were collected for this study. The line-intercept method (Canfield 1941) was used to estimate frequency of occurrence of shrubs and trees on the transects during each time period. During 1976–78 frequencies of occurrence of herbaceous species were estimated from five 0.1-m^2 circular plots spaced at 5-m intervals along each 25-m transect. Frequencies of occurrence of herbaceous species during 1985–87 were estimated from ten 0.5-m^2 circular plots spaced at 2-m intervals along each 20-m transect. N-tests were calculated during each time period to assure adequate sample sizes. Because plot sizes and number differed between time periods—factors that could affect absolute values of frequency of occurrence—a nonparametric Spearman rank correlation coefficient was used to test whether the seasonal and annual differences in the ranks of key foods available on WWA were mutually independent between 1976–78 and 1985–87. Dietary selection, defined as differential use and availability by comparison of the frequency of a particular food item in the diet to the frequency of occurrence from random vegetation sampling, was compared between time periods.

RESULTS

Key Foods

Fifty-three of approximately 90 plant taxa present on WWA were consumed by California Quail (39 taxa during 1976–78 and 44 taxa during 1985–87); 30 of the 53 foods were consumed during both time periods. Fourteen key plant foods were identified, 11 during 1976–78 and 13 in 1985–87 (Table 1). Quail consumed 10 of the same key foods during both periods. Bittercress was a key food only during 1976–78, and Scot's broom, deervetch (*Lotus* spp.), and sweet-clover (*Melilotus* spp.) were key foods only during 1985–87. All key foods, except grasses, were associated with disturbed areas or were exotic to western Oregon (Hitchcock and Cronquist 1973).

Thirteen key foods taken during 1985–87 composed 87% of the aggregate dry mass of crop contents. The four foods that constituted the greatest amount of the diet by mass were deervetch, peavine (*Lathyrus* spp.), Scot's broom, and vetch; these legumes made up 63% of the diet (Table 2). Other legumes in the diet (including clover [*Trifolium* spp.], sweet-clover, lupine [*Lupinus* spp.], and locust [*Robinia pseudo-acacia*]) collectively contributed an additional 4% of the diet. Grasses, which included 9 taxa but were primarily *Festuca* spp., *Dactylis glomerata*, and *Poa* spp., composed 8% of the aggregate dry mass, were present in the diet during each season, had the highest annual frequency of occurrence in the diet (84%), and were the most available food on the WWA (Table 3). The remaining key foods constituted 1–4% of the diet by aggregate dry mass.

Aggregate dry mass (%) of seeds and mature fruit pulp in the diet from 1985–87 was 49%, 95%, 97%, and 83% during spring, summer, fall, and winter, respectively; the remainder was foliage and flower parts (Table 2). Among the key foods, deervetch, peavine, and teasel were consumed only as seeds. Foliage and seeds of Scot's broom, vetch, grasses, wild carrot, clover, sweet-clover, and

TABLE 1. Annual and seasonal use (% frequency of occurrence) in crops of key plant foods of California Quail, E. E. Wilson Wildlife Area, Oregon, 1976–78 and 1985–87.

Food	Annual		Fall		Winter		Spring		Summer	
	1976–78 ($n = 117$)	1985–87 ($n = 105$)	1976–78 ($n = 50$)	1985–87 ($n = 56$)	1976–78 ($n = 30$)	1985–87 ($n = 17$)	1976–78 ($n = 12$)	1985–87 ($n = 19$)	1976–78 ($n = 25$)	1985–87 ($n = 13$)
Vetch	69	65	50	50	83	100	83	79	72	62
Grasses	38	81*	35	77*	27	100	33	79	56	100
Wild carrot	72	44*	56	25*	100	100	100	68	48	15
Teasel	31	45*	21	52*	60	71	42	21	4	15
Cichorieae	53	18*	38	4*	50	29	42	37	84	38
Sorrel	34	21	24	11	30	29	58	42	40	23
Deervetch	14	40*	6	41*	7	71	8	0	56	54
Peavine	31	20	26	25	53	24	33	16	8	0
Scot's broom	6	45*	12	34	0	41	8	74	4	54
Blackberry	17	31*	38	36	0	24*	0	11	16	54
Apple	22	23	9	39*	63	12*	0	0	0	0
Clover	19	22	0	4	13	59*	42	47	40	15
Bittercress	27	3*	3	0	47	6*	92	11	4	0
Sweet-clover	0	17*	0	13	0	35*	0	0	0	38

*Pairs of numbers from the two time periods were different ($P < .05$).

TABLE 2. Annual aggregate dry mass and plant parts consumed of key foods in crops of 105 California Quail, E. E. Wilson Wildlife Area, Oregon, 1985–87.

Food	Annual aggregate dry mass (%)	Plant parts consumed[a]			
		Fall ($n = 56$)	Winter ($n = 17$)	Spring ($n = 19$)	Summer ($n = 13$)
Deervetch	20	S	S	S	
Peavine	16	S	S	S	
Scot's broom	16	S,L	S,L	S,L,Fl	S,L,Fl
Vetch	11	S,L	S,L	S,L	S,L
Grasses	8	S,L	S,L	S,L	S,L
Wild carrot	4	S,L	S,L	S,L	L
Apple	3	Fr	Fr		
Clover	2	S,L	S,L	L	S,L
Blackberry	2	Fr	L,Fr	L,Fl	Fr
Teasel	2	S	S	S	S
Sweet-clover	1	S	S		S
Cichorieae	1	L,Fl	L	L,Fl	L,Fl
Sorrel	1	S,L	S,L	L	S
Other plant foods	13				

[a] S = seeds, L = leaves, Fl = flower parts, Fr = mature fruit or berry.

sorrel were taken by quail. Mature fruit, foliage, and flower parts of blackberries, the most abundant shrub on the WWA, were eaten. Quail also used foliage and flower parts of Cichorieae and pulp of apples. Parts of the key foods consumed during 1976–78 and 1985–87 were identical.

Use and Availability

Frequencies of nine key plant foods in the diet of California Quail differed ($P < .05$) between 1976–78 and 1985–87 (Table 1). Deervetch, Scot's broom, sweet-clover, grasses, teasel, and blackberry increased in frequency of occurrence. Use of wild carrot, Cichorieae, and bittercress decreased. Most differences in seasonal frequencies of use between 1976–78 and 1985–87 occurred during fall and winter (Table 1) compared with spring and summer. Grasses, wild carrot, and vetch were present in >33% of all crops during both collection periods, but Cichorieae and sorrel were replaced by deervetch, Scot's broom, and teasel among the high-frequency foods during 1985–87.

Availabilities of the most common foods (grasses, blackberry, vetch, and wild carrot) and availabilities of the least common key

TABLE 3. Annual and seasonal availability (% frequency of occurrence in habitat) of key plant foods of California Quail, E. E. Wilson Wildlife Area, Oregon, 1976–78 and 1985–87.

	Annual[a]		Fall[a]		Winter[a]		Spring[a]		Summer[a]	
Food	1976–78	1985–87	1976–78	1985–87	1976–78	1985–87	1976–78	1985–87	1976–78	1985–87
Grasses	92	92	90	94	91	90	93	91	96	92
Blackberry	53	60	55	60	53	62	51	60	51	57
Vetch	53	40	61	34	48	52	53	59	58	17
Wild carrot	27	35	28	26	15	34	33	44	42	36
Teasel	9	20	10	21	8	15	10	26	9	20
Cichorieae	6	11	9	10	5	16	5	10	4	9
Apple	7	1	5	3	6	0	7	8	10	5
Scot's broom	4	6	1	13	5	8	5	3	4	3
Sorrel	3	5	3	5	4	8	4	3	3	4
Bittercress	3	2	1	1	5	5	4	3	1	0
Clover	2	2	1	3	1	2	2	3	2	1
Peavine	1	3	1	2	1	3	1	3	1	3
Deervetch	1	2	1	2	1	1	2	4	1	3
Sweet-clover	1	1	1	1	0	0	0	0	0	0

[a] Relative rankings of availabilities of key foods did not not differ ($P < .005$) between time periods.

foods (peavine, deervetch, clover, and sweet-clover) were similar between periods (Table 3). Results of the rank correlation revealed that relative availabilities of key foods were similar ($P < .005$) between 1976–78 and 1985–87.

Legumes were prominent among the key foods with the highest frequencies of consumption and lowest availabilities in the habitat (Tables 1, 3) and, consequently, were identified as some of the most highly selected foods. Six foods occurred in greater frequencies in the diets of quail than they were available at random locations in the shrub/grassland habitat in ≥ 1 season during both 1976–78 and 1985–87. These foods included peavine, clover, deervetch, Scot's broom, sorrel, and apple. Bittercress and Cichorieae were differentially used only during 1976–78, and sweet-clover only during 1985–87. Three of the most highly selected (those with the greatest differences between use and availability) foods (deervetch, peavine, and Scot's broom) collectively provided 52% of the diet by aggregate dry mass during 1985–87. Vetch, grasses, and wild carrot, which contributed 23% of the diet by mass, were consumed in relatively high frequencies but were abundantly available throughout the habitat. The remaining 25% of the diet was made up of a large number of foods, most of which were available in low frequencies and individually provided only a small amount of the diet by mass.

DISCUSSION

We concluded that California Quail at the WWA consumed many of the plant foods available on the area but that they selectively consumed a relatively small group of foods, especially legumes. However, there were significant differences in diets of the quail between 1976–78 and 1985–87. Most differences in seasonal frequencies of use occurred during fall and winter. A greater variety of foods typically is available during fall and winter (Gullion 1966, Leopold 1977:170), and differences possibly reflected greater opportunity for selection of foods by quail during these seasons. Apparently, California Quail were not particularly selective and therefore more opportunistic within the key group of foods because 9 of the 14 key foods were consumed in different frequencies between the two time periods, without apparent changes in availability (the mesic environment of western Oregon apparently provided relatively consistent availability of plant foods).

The diets of California Quail at WWA contained both specialist and generalist elements: approximately one-half the diet was composed of a few highly selected foods with very low availabilities, one-fourth was made up of several widespread, abundant items, and one-fourth consisted of a large number of locally available foods. We interpreted these results to reflect a diet wherein quail sought out areas of highly selected foods and optimized their foraging time and efficiency by consuming locally abundant key foods at these sites.

Legumes were moderately to highly used, composed 63% of the diet by mass during 1985–87, and, in most instances, were eaten in substantially greater frequencies than they occurred in the habitat. Erwin (1975) suggested a relationship between breeding activity and legume consumption in California Quail. Further, Browning (in Leopold 1977:230) stated that availability of legume seeds was a primary factor in high production during wet years in arid ranges in California. Oates and Crawford (1983) reported that legumes (except vetch) were related to the distribution and productivity of quail in western Oregon. In arid portions of the range of California Quail, filarees, cultivated grains, legumes, grasses, and a variety of fruits from trees and shrubs were reported as staple foods (Sumner 1935, Glading et al. 1940, Crispens et al. 1960). Johnsgard (1973:398) concluded that legumes were the most preferred foods of California Quail in their native range but probably were less important in extralimital populations. In western Oregon, a mesic extension of the range of California Quail, our study indicated that legumes were the most important foods.

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WINTER MORTALITY OF THE RUSSIAN WHEAT APHID (HOMOPTERA: APHIDIDAE) ON RANGE GRASSES IN NORTHERN UTAH

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Key words. Russian wheat aphid, grasses, rangelands, winter mortality.

The Russian wheat aphid, *Diuraphis noxia* (Mordvilko), is a newly established pest of small grains in western North America (Stoetzel 1987). This aphid also feeds on several native and introduced grasses, including grasses that are widely planted for forage improvement or erosion prevention in rangelands (Kindler and Springer 1989, Kindler et al. 1991). Recent attention has focused on the potential importance of these grasses as "oversummering" hosts for *D. noxia*, i.e., as sources of aphid populations between the summer harvest and fall sowing of winter wheat, *Triticum aestivum* L. (Clement et al. 1990, Armstrong et al. 1991). Comparatively little information is available on the role of grasses as overwintering sites, even though migrants from noncrop hosts could cause extensive damage to cereals in the spring. In this study I investigated the overwintering success of the Russian wheat aphid on cool-season grasses in northern Utah.

The ability of *D. noxia* to survive winter conditions varies regionally in North America. Winter mortality may reach 100% at higher latitudes (Butts 1992), so that aphid populations must be reestablished by migrants each season. Such high mortality may stem from a lack of sexual reproduction (anholocycly) in North American populations (Kiriac et al. 1990, Stoetzel and Hammon 1992), since a sexual generation in the fall is needed to produce the cold-hardy egg stage. Parthenogenetic females of *D. noxia* are quite cold-hardy (Harvey and Martin 1988), however, and occasionally survive winter conditions in northern regions, including Colorado, Idaho, and Alberta (Butts 1992, Feng et al. 1992, Hammon and Peairs 1992).

The overwintering success of *D. noxia* in northern Utah has not been investigated, but the typical absence of aphids in early spring suggests that fall populations are eliminated during most winters. In October 1991 I detected a population of *D. noxia* on cool-season grasses in an experimental garden near Utah State University. I surveyed this population throughout the winter and compared the pattern of mortality with local temperature data.

MATERIALS AND METHODS

A common garden of six native and introduced grass species (Table 1, nomenclature follows Barkworth and Dewey 1985) was established in 1990 at the Greenville Experimental Farm in North Logan, Utah. The garden consisted of 432 plants in six blocks, with 12 plants per grass species per block. All plants had produced flowering culms and large tussocks by early October 1991, at which time damage caused by the Russian wheat aphid (e.g., necrotic streaks on leaves) became apparent on several individuals. Further inspection confirmed the presence of Russian wheat aphids within the tightly rolled leaves of the newly produced fall (overwintering) tillers.

I estimated the initial extent of the aphid infestation on 15 October 1991 by collecting five tillers from each of 18 randomly chosen plants per grass species. Samples were transported to the laboratory in plastic bags and maintained at 5°C for later examination. I recorded aphid density as 0, 1–100, or >100 individuals per five tillers. I also noted any winged (alate) adults or nymphs bearing wing pads. Thirty-six of the original 108 plants (6

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TABLE 1. Number of plants from six grass species bearing 0, 1–100, or >100 *D. noxia* aphids per five tillers in October 1992.

	Aphid density class		
Host species (cultivar)	0	1–100	>100
Agropyron desertorum (Fischer ex Link) Schultes (crested wheatgrass, 'Nordan')	5	11	2
Elymus lanceolatus (Scribner & J. G. Smith) Gould (Snake River wheatgrass, 'Secar')	8	10	0
Leymus cinereus (Scribner & Merrill) A. Löve (Great Basin wildrye, 'Magnar')	7	11	0
Oryzopsis hymenoides (Roemer & Schultes) Ricker (Indian ricegrass, 'Paloma')	1	16	1
Pseudoregneria spicata (Pursh) A. Löve (bluebunch wheatgrass, 'Whitmar')	11	7	0
Thinopyrum intermedium (Schur) Barkw. & D. R. Dewey (intermediate pubescent wheatgrass, 'Luna')	5	12	1

per grass species) were then chosen for monthly samples from November 1991 to April 1992 (dates are listed in Table 2). On each sampling date I clipped 10–20 tillers per plant, sometimes after brushing away snowcover. In the laboratory I recorded the presence of any live aphids, which were so determined by the retention of a pale green body color and the independent movement of one or more appendages. A wider sample of plants was obtained on 8 and 21 April 1992; I pooled tillers from ≥ 10 individual plants per grass species so as to fill two 4-L plastic bags.

Daily temperature data from October to April were supplied by the Utah Climate Center, which maintains a weather station at Greenville Farm. To estimate the severity of winter conditions during the sampling period, I compared 1991–92 temperature records on the Utah State University campus (which is <2.5 km from Greenville Farm) with long-term (30-yr) averages from the same site.

RESULTS

The initial census in October indicated that aphids had infested all six species of cool-season grasses, with a few plants bearing >100 aphids per five tillers (Table 1). The proportion of plants infested varied significantly among grass species ($X^2 = 14.0$, df = 5, $P < .02$); virtually all of the Indian ricegrass plant bore aphids, while Russian wheat aphids were found on less than half of the bluebunch wheatgrass plants. Alate adults were found on only 5 of 108 plants, but nymphs bearing wing pads were common on all host species. Prior to this initial census, daily minimum temperature had dropped below freezing (down to –1°C) on only a single date (Fig. 1).

Live aphids remained abundant on each grass species on 19 November (Table 2), despite several days of sub-zero minimum temperatures in late October and early November (including a reading of –16°C on 3 November). On 6 December, 5 days after the minimum temperature had dropped to –20°C, each sample contained many dead aphids, but at least a few live aphids were found on all hosts except Indian ricegrass. No winged adults were found on this date or on any subsequent date.

Four hosts bore live aphids in early January, but only two (crested wheatgrass and intermediate pubescent wheatgrass) still did so by mid-February (Table 2). Very cold temperatures were recorded between these two sampling dates, including a seasonal low of –26°C on 21 January (Fig. 1). Most live aphids in the mid-February samples appeared to be in a torpid condition and were unable to right themselves or walk normally. Ten aphids that appeared to walk normally were placed on winter wheat seelings ('Hansel' variety) at room temperature (these seedlings were known to support a thriving laboratory colony of *D. noxia*). Although a few aphids probed the leaves and assumed a feeding stance, all were dead within 48 h.

Daily maximum and minimum temperatures were unseasonably high after the February samples were taken, and temperatures remained high throughout the early spring (Fig. 1). Despite this apparent improvement in

TABLE 2. Presence (+) or absence (–) of live *D. noxia* aphids from six grasses sampled from November 1991 to April 1992.

Host[a]	19 Nov	6 Dec	3 Jan	11 Feb	11 Mar	2 Apr	8 Apr	21 Apr
Crested wheatgrass	+	+	+	+	+	–	–	–
Snake River wheatgrass	+	+	–	–	–	–	–	–
Great Basin wildrye	+	+	+	–	–	–	–	–
Indian ricegrass	+	–	–	–	–	–	–	–
Bluebunch wheatgrass	+	+	+	–	–	–	–	–
Intermediate pubescent wheatgrass	+	+	+	+	–	–	–	–

[a] Full descriptions in Table 1

ambient temperature, only crested wheatgrass bore live aphids by mid-March, and no live aphids were found on any host in early April (Table 1). This local extinction was confirmed by the more widespread surveys on 8 and 21 April, and no aphids were observed during experiments in the garden from May to July 1992. Monthly averages of daily minimum temperatures in 1991–92 suggested that the extinction of the aphid population occurred during a fairly typical winter. Average temperatures from November to January were only slightly below long-term averages, and the period from February to April (which included the last dates when live aphids were observed) was significantly warmer than usual (Table 3).

DISCUSSION

This survey suggests that parthenogenetic Russian wheat aphids cannot survive typical winter temperatures in northern Utah. Nevertheless, aphids may survive winters that are warmer than usual, as low numbers of live aphids were recovered as late as mid-March in 1992. A small fraction of an aphid population on wheat did survive winter conditions in 1989–90 (but not 1988–89) in southern Alberta, where temperatures are generally colder than those in northern Utah (Butts 1992). Similarly, aphids apparently persisted through the winter of 1987–88 in southwestern Idaho but were not detected after mid-December in the colder, early winter of 1988–89 (Feng et al. 1992). Further research is needed to assess how other abiotic factors (e.g., snowcover or humidity) may modify the effect of temperature on aphid survival.

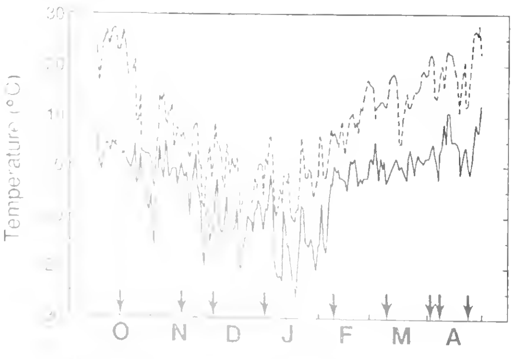

Fig. 1. Daily maximum and minimum temperatures, October 1991 to April 1992, at Greenville Farm. Arrows indicate dates [illegible] sampled for aphids.

The overwintering success of *D. noxia* on cool-season grasses may also depend on host species. The temporal pattern of mortality in 1991–92 appeared to reflect the differing growth forms of the six hosts in the experimental garden. Indian ricegrass yielded no live aphids as early as 6 December, even though this host bore the most widespread infestation in October (Tables 1, 2). Because Indian ricegrass produces very thin shoots that are arranged in a sparse, open tussock, it is expected to render little protection to aphids beyond that provided by the individual rolled leaf. In contrast, the extremely dense, compact tussocks of crested wheatgrass should provide a substantial buffer from either cold injury or desiccation, and this species was the last host to yield live aphids. Intermediate pubescent wheatgrass also produces relatively dense tussocks and harbored live aphids until mid-February (Table 2). In general, winter survival of parthenogenetic *D. noxia* in North America may depend on a complex interaction between climatic conditions and host type. Young winter wheat

TABLE 3. Mean daily minimum temperatures (°C) per month from October to April 1991–92 and over the previous 30 yr at Logan, Utah.

	Mean minimum temperature	
Month	1991–92	Long-term (± SD)
October	6.7	3.6 ± 1.6
November	−2.1	−2.0 ± 1.4
December	−9.1	−7.9 ± 2.4
January	−11.0	−9.3 ± 3.1
February	−3.5	−6.8 ± 3.3
March	2.3	−2.4 ± 2.1
April	5.9	2.1 ± 1.7

plants would probably provide less protection than most of the mature tussock grasses studied here.

It was anticipated that the live aphids recovered in mid-March would produce a significant infestation of grasses in the spring, since temperatures never dipped much below 0°C for the remainder of the early spring (Fig.1). The apparent extinction of the population suggests that aphids classified as alive in February and March had already suffered irreversible cold injury and were incapable of resuming feeding and development when temperatures increased. This hypothesis was also supported by the high frequency of torpid aphids in the February sample and the rapid mortality of aphids placed on wheat seedling in the laboratory. Caution is therefore required in inferring overwintering ability or in forecasting spring infestations from simple live or dead determinations. Finally, this survey supports the contention of Butts (1992) that the overwintering success of *D. noxia* cannot be predicted simply from the aphid's supercooling point of ca. −25°C. Aphids suffered complete mortality on Indian ricegrass and Snake River wheatgrass, for example, well before ambient temperature approached the supercooling value (Table 2, Fig.1). It is interesting to note that Indian ricegrass is a relatively poor overwintering host for *D. noxia* but a consistently superior summer host (Table 1, and unpublished data).

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PREDATION BY OSPREY ON ENDANGERED HUMPBACK CHUB

Anthony Wasowicz[1] and Helen Yard[1]

Key words. humpback chub, Gila cypha, *Osprey,* Pandion haliaetus, *Grand Canyon, Colorado River, Little Colorado River, predation.*

The humpback chub (*Gila cypha*) is a large-river cyprinid endemic to the Colorado River Basin and is federally protected by the Endangered Species Act of 1973. Currently, only five populations are known, each in isolated canyon areas of the Colorado River and its tributaries (Valdez and Clemmer 1982). In the Grand Canyon a viable population occurs within a 12-km reach centered near the confluence of the Colorado and Little Colorado rivers. The chub spawn in the Little Colorado River (LCR) in early summer and are dispersed in the mainstem the remainder of the year (BIO/WEST, unpublished data). There also appears to be a resident population of chubs in the LCR.

Direct observation of avian predation on fish is common, especially for trout (e.g., Anderson et al. 1974, Wasowicz 1991). Although numerous potential predators exist in the Grand Canyon, direct observation of bird predation on humpback chub has never been reported.

Avian piscivores in the Grand Canyon include waterbirds such as herons, gulls, and mergansers, as well as raptors such as eagles and ospreys. Bald Eagles (*Haliaeetus leucocephalus*) have been observed congregating at Nankoweep Creek (52.1 miles downstream from Lee's Ferry) in late winter to feed on rainbow trout (*Oncorhynchus mykiss*) moving into the creek from the mainstem to spawn.

Osprey (*Pandion haliaetus*) are considered "rare-transients" in the Grand Canyon, utilizing marsh open water and riparian habitat as they pass through the canyon as migrants in the spring and/or fall (Brown et al. 1981). Most North American ospreys are migratory, wintering in Latin America and the Caribbean Basin with concentrations in northern South America (Poole 1989).

On 6 September 1991 we observed an adult Osprey flying over the mainstem Colorado upstream with a fish in its talons. We had a clear view of the prey as the bird passed overhead along the shoreline at low level. The fish was positively identified as an adult humpback chub by its distinct deep body shape, its elongated, slender caudle peduncle with a deeply forked tail, and its light gray color. This observation occurred at river mile 57.1, about 6.9 km upstream of the confluence with the LCR. It is not known whether the chub was taken in the mainstem Colorado River or in the LCR.

It is likely that the Osprey captured, rather than scavenged, the fish. With rare exceptions, Osprey catch and eat live fish only. Poole (1989) found that live fish comprised over 99% of the diet of Osprey populations reviewed in literature. Osprey regularly scavenge carcasses for nesting material (Poole 1989), but these birds do not nest in the Grand Canyon.

Further possible evidence of avian predation had been discovered several months prior to this observation. On 14 May 1991 a radiotransmitter, which was previously implanted by BIO/WEST biologists into an adult humpback chub, was discovered on the bank of the LCR, approximately 30 m from the confluence. The transmitter was found among boulders, 3–4 vertical meters above the water surface. No remains of the fish were located in the area, but one white feather was found stuck to the transmitter. An Osprey was observed frequenting the LCR confluence area on 12 and 13 May. We believe this fish

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[1] BIO/WEST, Inc., 106[illegible]

was taken by an Osprey, rather than found dead and removed from the water by a scavenger (e.g., coyote, raven, ringtail). Before its tag was discovered on the bank, the fish was successfully monitored for three months following implanting and had moved nearly one mile to the confluence and then up the LCR, indicative of a healthy fish. To date, we have never discovered a dead ("floater") fish out of 75 implanted humpback chub monitored for 6–12 days every month but December. Also, humpback chubs staging at the confluence, prior to migration up the LCR to spawn, were observed swimming near the surface of the water in May. Osprey can forage only to about 1 m below the water's surface and therefore are able to catch fish only near the surface of the water (Poole 1989).

ACKNOWLEDGMENTS

This observation was made during an investigation of the life history and ecology of the humpback chub in the Grand Canyon by BIO/WEST, Inc. The study was funded by the Bureau of Reclamation (Contract No. 0-CS-40-09110), in cooperation with Glen Canyon Environmental Studies and Grand Canyon National Park. We wish to thank Dr. Richard Valdez for helpful suggestions that improved the manuscript, and William Masslich for providing supplemental information.

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TRANSPORT OF A JUVENILE PINYON MOUSE (*PEROMYSCUS TRUEI*)

J. R. Callahan[1] and Daniel S. Compton[2]

Key words: Peromyscus, *transport, clinging, juvenile, predator.*

On 18 July 1992 we observed an interesting mode of transport of a juvenile pinyon mouse (*Peromyscus truei*) by an adult female presumed to be its parent. The habitat was transitional between *Arctostaphylos/Ceanothus/Quercus* chaparral and mixed conifer forest in the San Jacinto Mountains, Riverside County, California, elevation 2100 m. We had been observing a 75-cm western rattlesnake (*Crotalus viridis*) that emerged from a burrow at 4:30 PM, remained stationary for a few minutes, and then moved directly to a fallen log 12 m away. Within 20 seconds after the snake went under the log, a small mammal emerged, moving at high speed. The mammal ran 8 m to a scrub oak (*Quercus dumosa*) and climbed to a limb 80 cm aboveground. While it was running, we had the impression of a grayish rodent 7–8 cm in head-body length, with large ears and a very bushy tail. Since no such mammal occurs in the area, we investigated further.

After approaching to within 30–40 cm, we observed an adult female pinyon mouse standing on the limb, with a juvenile (the large "tail" we had seen) firmly attached by its mouth to the nipple of one of the female's left inguinal mammae. The juvenile's eyes were open and its body mass appeared to be 0.40 that of the adult. It had gray juvenile pelage and appeared less than 3 weeks old. While the female turned her head back and forth and shifted position on the branch, the juvenile remained motionless beside her. There was no evidence of injury to either animal. After a few minutes, the female ran down the shrub to the ground, still dragging the juvenile bouncing along behind her. She then darted 4 m to a different log and began digging at its underside, sending fragments of rotten wood and loam flying in all directions. Both mice were concealed within minutes.

"Nipple clinging" behavior has been reported for several species of *Peromyscus*, but we could find no published discussion of the phenomenon more recent than Layne (1968). Guetzow and Judd (1981) noted the onset of clinging as a developmental milestone in juvenile *P. leucopus*, but did not discuss its adaptive significance. This behavior apparently has received little field study; laboratory experiments have shown that it varies with age and species (King 1963), and that it may be related to emergency evacuation of the nest. Layne (1968) wrote:

> The principal adaptive value of nipple clinging is probably reduction of litter losses through predation, although this assumption cannot presently be supported with good observational or experimental evidence.

Rand and Holt (1942) wrote that the behavior

> may be of some importance . . . when the nest is threatened by an invading enemy, as for instance, a snake. Our experience when excavating burrows, however, did not give too much support to this.

Their hypothesis apears to be supported by our field observation reported here. Nipple-clinging behavior has been reported for certain other rodent genera, such as *Neotoma* (Hamilton 1953). Davis (1970) reviewed the literature on similar emergency transport of young by flying female bats.

Layne (1968) noted that clinging behavior by older juvenile *Peromyscus* sometimes occurs in non-emergency situations, as when the mother and young are foraging together. In this context, the attached juvenile walks

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[2] [illegible]

behind the female rather than being dragged along. This behavior may explain the following related observation. Between 30 June and 10 July 1992 we conducted a mark-and-recapture study of small mammals in Riversidean sage scrub and alluvial scrub habitat just south of Highland, San Bernardino County, California. One 9-inch folding Sherman trap was found to contain two dead cactus mice (*Peromyscus eremicus*): a 3- to 4-week-old juvenile whose neck had been caught in the trap door, with its head inside the trap and the body hanging outside; and a lactating adult female, with one foot caught under the treadle and some caked blood on its venter. The adult was a recapture from the previous night; the juvenile was not marked. The most likely scenario is that the juvenile was clinging to the female's nipple when she entered the trap. The door apparently then slammed shut on the juvenile's neck, tearing it off the female. The use of longer Sherman traps (Slade et al. 1993) is recommended to reduce the incidence of this and other categories of trap injury.

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EVIDENCE OF *BISON BISON* IN THE GREAT BASIN

Dirk Van Vuren[1] and Frank C. Deitz[2]

Key words. Bison bison, *bison, Great Basin, biogeography, archaeology.*

The former occurrence of modern bison (*Bison bison*) in the Great Basin is poorly understood yet is of considerable importance in understanding the biogeography (Berger 1986:248) and archaeology (Butler 1978) of the area. Bison occurred at the northern edge of the Great Basin, around Malheur Lake (Bailey 1936, Van Vuren and Bray 1985) and at the eastern edge, near Great Salt Lake (Durrant 1952). Reports of bison skulls from the central part of the Great Basin, however, are lacking except for the partial skull of a male recovered in Lander County, Nevada, in 1955 (Hall 1961). This report is problematic because the locality is ca. 400 km distant from either Malheur Lake or Great Salt Lake (Fig. 1). Does this specimen represent a lone individual that wandered a great distance, or was it a member of a viable population of bison living in northern Nevada? The former existence of a population of bison in northern Nevada, particularly in the Humboldt River Valley, has long been suspected (Steward 1938:38, Hall 1946:644) but never substantiated. Herein we report the discovery of two more bison skulls from the Great Basin, both from near the Humboldt River in northeastern Nevada.

In 1990 the partial skull of a male bison, consisting of horn cores and the cranium posterior to the orbits, was found in an ephemeral wash 35 km NE of Wells, Elko County (41°21'10"N, 114°42'8"W). No other bones or cultural materials were found in association with the skull.

In 1992 Bureau of Land Management (BLM) wildlife biologists discovered the complete skull of a female bison embedded at a depth of [illegible] m in a cut bank of Susie Creek, a perennial [illegible] km NNE of Carlin, Elko County ([illegible]8"N, 116°2'18"W). At the time of discovery, a fragment of the skull was dislodged; a chert (cryptocrystalline silicate) scraper fell simultaneously with the fragment, suggesting that the skull and scraper were associated.

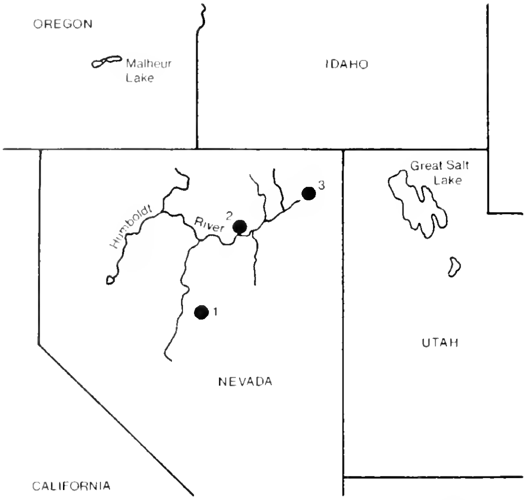

Fig. 1. Localities of bison skulls reported from Nevada: (1) a male (Hall 1961), (2) a female (this report), and (3) a male (this report).

The site (26EK5465) was investigated by BLM archaeologists, and the skull was excavated with no finding of additional bison remains. Other artifacts found within 15 cm of the skull were two chert flakes and a possible battered cobble. One of the flakes is of the same chert as the scraper, further supporting an archaeological association between skull and stone tools. The general area has numerous archaeological and faunal remains, both surface and subsurface, and few have received more than cursory attention. One charcoal sample situated 62 cm directly above the skull was submitted for radiocarbon dating using

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[1] Departme[illegible] of California, Davis, California 95616
[2] U.S. Bureau [illegible] 89803

the accelerator mass spectrometry technique (Beta Analytic, Inc., Miami, Florida). Adjusted age was 950 ± 60 yr BP (Beta-55584 ETH-10033).

Standard measures (Skinner and Kaisen 1947:145) of each skull did not differ significantly ($P > .05$, modified t test, Sokal and Rohlf 1981:229–231) from measures of *Bison bison* given by McDonald (1981:96). Standard measures of the skulls are available, upon request, from the senior author. Both skulls are currently curated at the U.S. Bureau of Land Management, Elko District Office, Elko, Nevada. The Susie Creek specimen will be permanently housed at the Nevada State Museum, Carson City.

All three specimens of bison reported from Nevada were recovered in or near the basin drained by the Humboldt River (Fig. 1), an area that currently supports thousands of cattle and probably provided suitable habitat for bison. Although male bison may spend much of the year alone (McHugh 1958) and sometimes wander substantial distances from other bison (McHugh 1958, Meagher 1989), females are highly gregarious (McHugh 1958). Thus, the occurrence of a female in addition to two males suggests that a breeding population of bison may have inhabited the Humboldt River drainage of northeastern Nevada.

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Roy Price and Carol Evans discovered the Susie Creek skull. Bryan Hockett and Tim Murphy supported and assisted in the investigation and excavation, and Robert Bettinger gave sound advice.

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SEASONAL TRENDS AND COLONIZATION PATTERNS OF MACROINVERTEBRATE ASSEMBLAGES IN TWO STREAMS WITH CONTRASTING FLOW REGIMES

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and Lynn Van Every[2]

Abstract.—Patterns of colonization by macroinvertebrates were examined in two streams that differ in flow regime: a snowmelt system and a mesic groundwater system. Experiments were conducted during spring runoff, summer baseflow, and winter baseflow using artificial substrata. Colonization patterns reflected seasonal changes in benthic macroinvertebrate assemblages and life histories in each stream. The density and biomass of benthic organisms were approximately 3X greater in winter than in either spring or summer for both streams. Similarly, colonization was greater in winter than in spring or summer for both streams. In spring, colonization patterns were different between streams, with colonization being imperceptible in the snowmelt stream. Macroinvertebrate abundance fluctuated during the summer colonization experiment at both sites, resulting from a complex interplay among population emergence, recruitment, and/or movement. Assemblages in the snowmelt system primarily comprised mobile or ruderal taxa, such as *Baetis tricaudatus* and Chironomidae, whereas relatively sessile taxa, such as *Glossosoma nigrior*, were predominant in the mesic groundwater system. Seasonal patterns of colonization differed among stream types primarily because of the profound interplay of flow regime and temperature on benthic community structure and organism life history.

Key words: colonization, streams, life history, flow regime, macroinvertebrates, Idaho, seasonality

Colonization of denuded substrata or disturbed habitats by lotic macroinvertebrates has been an intensively studied process, as shown by the extensive review of Mackay (1992). Experiments on colonization can provide insights about important factors that influence stream structure and function, such as seasonality (Williams 1980, Robinson et al. 1990), life history dynamics (Diamond and Reice 1985), and biotic and abiotic structuring mechanisms (McArthur and Barnes 1985, Minshall and Petersen 1985, Minshall 1988, Poff and Ward 1989, Kohler 1992, Power 1992). In addition, insights gained from colonization studies are directly applicable in examining the recovery dynamics of macroinvertebrate communities following disturbance at various spatio-temporal scales (Minshall and Petersen 1985, Minshall 1988, also see references in Mackay 1992).

Flow variability and predictability have been hypothesized to be major components of the habitat templet (sensu Southwood 1977, 1988) for lotic macroinvertebrate communities

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by dictating the kinds, numbers, and life history strategies of organisms present (Minshall 1988). For example, Minshall (1988) suggested that so-called r-strategists should predominate in streams with an unpredictable flow regime, whereas so-called K-strategists should be predominant in streams having a relatively constant flow regime. Poff and Ward (1989) expanded on these ideas in developing a classification system for streams based on flow regime and further explored the implications in terms of benthic community structure. Consequently, patterns of colonization should differ among streams that differ in flow regime because of inherent differences in benthic community structure, such as the differential composition of organism life histories. We have demonstrated elsewhere that the predominance and abundance of species with either r- or K-adapted life history strategies differ between a stream having constant discharge and one having seasonal variations in flow (e.g., that the ratio of r-strategists to K-strategists varies depending on the amount of environmental heterogeneity associated with seasonal variations in discharge; Minshall 1988, Robinson 1992). The present study examined seasonal colonization patterns in the same two adjacent streams differing in flow variability but having relatively high levels of predictability: one stream experiences spring runoff from snowmelt at about the same time each year, while the other stream has a seasonally constant flow regime (Robinson 1992, Robinson et al. 1992).

Seasonal fluctuations in macroinvertebrate abundance are well documented for streams in temperate regions. These fluctuations in abundance have been ascribed to life history adaptations to seasonal changes in temperature, photoperiod, food resources, and even leaf fall (Clifford 1978, Hart 1985, Robinson and Minshall 1986, Benson and Pearson 1987, Mackay 1992). There have been contrasting findings on the degree of concordance of benthic assemblage structure with respective assemblage structure on substrata used in colonization studies (Williams 1980, Ciborowski and Clifford 1984, Benson and Pearson 1987). In addition, there is a growing awareness that the importance of biotic factors, such as competition and predation, may vary seasonally (McAuliffe 1984, Bruns and Minshall 1986, Kohler 1992). Based on these observations, one might reasonably expect that patterns of colonization, in general, and recolonization following physical disturbance, in particular, may vary depending on the relative effects of biotic and abiotic factors and benthic abundances among seasons (Rabeni and Minshall 1977, Shaw and Minshall 1980, Minshall and Petersen 1985, Robinson and Minshall 1986, Robinson et al. 1990). Thus, we posit that the colonization process, in general, and recolonization following physical disturbance, in particular, will differ seasonally between these two types of streams, with streams populated by predominantly r-adapted species showing more rapid recolonization following disturbance than streams in which K-adapted species predominate. As background to these experiments, we also describe and relate seasonal trends in benthic macroinvertebrate assemblages found in each stream to assemblages colonizing the experimental substrata.

This study examined colonization at three times (summer, winter, and spring) during a 1-year period, thus incorporating seasonal changes in life histories and benthic abundance between the two study streams. We hypothesize that seasonal colonization dynamics should reflect the life history attributes of the macroinvertebrate assemblage present in each stream as a result of temporal differences in habitat templet (Minshall 1988). We expect colonization patterns to be different in spring, but similar during summer and winter, because flow regimes are different and similar at those times, respectively.

METHODS

Study Streams

The study was conducted in Birch Creek (112°57'W, 44°14'N) and Little Lost River (113°20'W, 44°20'N), Lemhi County, Idaho. Birch Creek (Birch) and Little Lost River (Lost) are two adjacent strea about apart. The two basins are sep 3200-m-high Lemhi Mountain sites were chosen at similar elevation m at Birch, 2046 m at Lost). The primary physical difference between Birch and Lost is the annual flow regime, although maximum spring water temperatures were higher in Birch than in Lost (Fig. 1). Mean monthly discharge was 1.16–1.65 m^3/s in Birch (annual flow CV

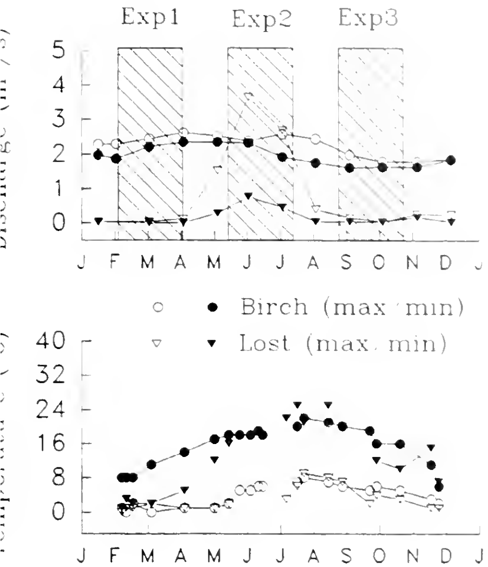

Fig. 1. Maximum and minimum discharge and temper- ure regimes for Birch Creek and Little Lost River dur- g the year of study. Cross-hatched boxes represent peri- ls when colonization experiments were conducted.

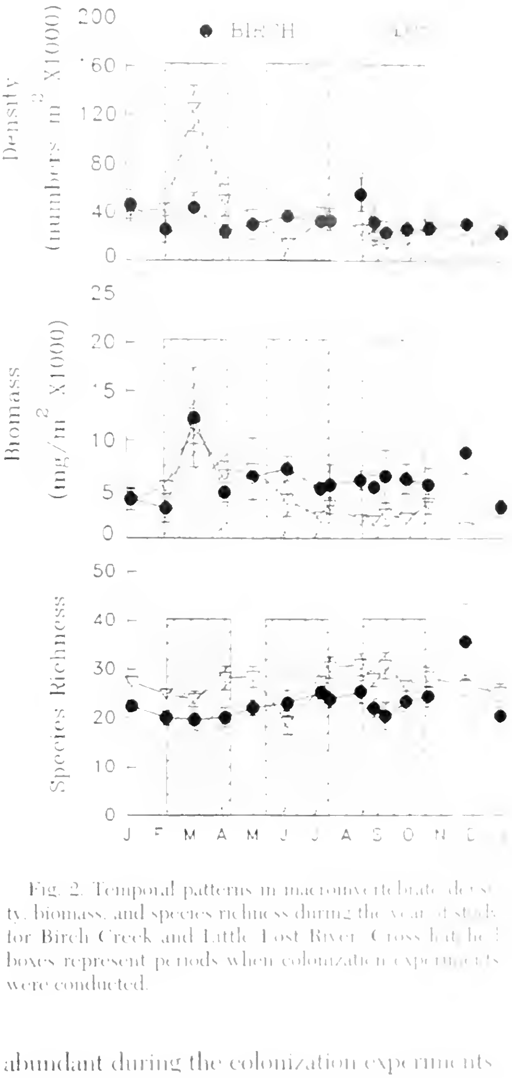

Fig. 2. Temporal patterns in macroinvertebrate density, biomass, and species richness during the year of study for Birch Creek and Little Lost River. Cross-hatched boxes represent periods when colonization experiments were conducted.

= 12%) and 0.001–1.37 m^3/s in Lost (annual ow CV = 114%). Robinson et al. (1992) pro- ide a complete description of the study sites.

Field Collections

SEASONAL TRENDS OF BENTHIC MACROIN- ERTEBRATE ASSEMBLAGES.—Benthic macro- nvertebrates were sampled randomly from ne same five riffle/run habitats each month sing a modified Hess sampler (250 μm mesh; = 5/month/stream). Sampling was initiated n 1 January 1988, and the final set of benthic amples was collected on 22 January 1989. ontents from each sample were preserved in ne field with formalin (10%). In the laborato- all macroinvertebrates were handpicked sing a dissecting microscope (10X), identi- lowest actical taxonomic unit, enu- d at 60°C for biomass deter- iomass was determined with a lectrobalance (Model 25) to the near- st microgram.

Data were used to calculate seasonal differ- nces in community density (no./m^2), biomass ng/m^2), and taxa richness for each stream. In ddition, temporal trends in density and bio- nass of six selected taxa found to be most abundant during the colonization experiments described below, also were determined from these samples: *Antocha* sp., *Baetis tricaudatus*, Chironomidae, *Ephemerella inermis*, *Glossosoma nigrior*, and Simuliidae. Data were transformed (log x+1) to correct for normality and tested for differences using analysis of variance and Tukey's post-hoc means test (Zar 1984, Statsoft 1990). In the following text species will be referred to by genus for brevity.

SEASONAL COLONIZATION EXPERIMENTS.— Forty unglazed half-bricks (20 × 9 × 2.5 cm) were placed in each stream and allowed to colonize at least 30 days prior to each experiment to allow development of a periphyton film (Robinson et al. 1990). Experiments were conducted during three seasons. Experiment 1 was from 6 February 1988 to 2 April 1988 ("winter"

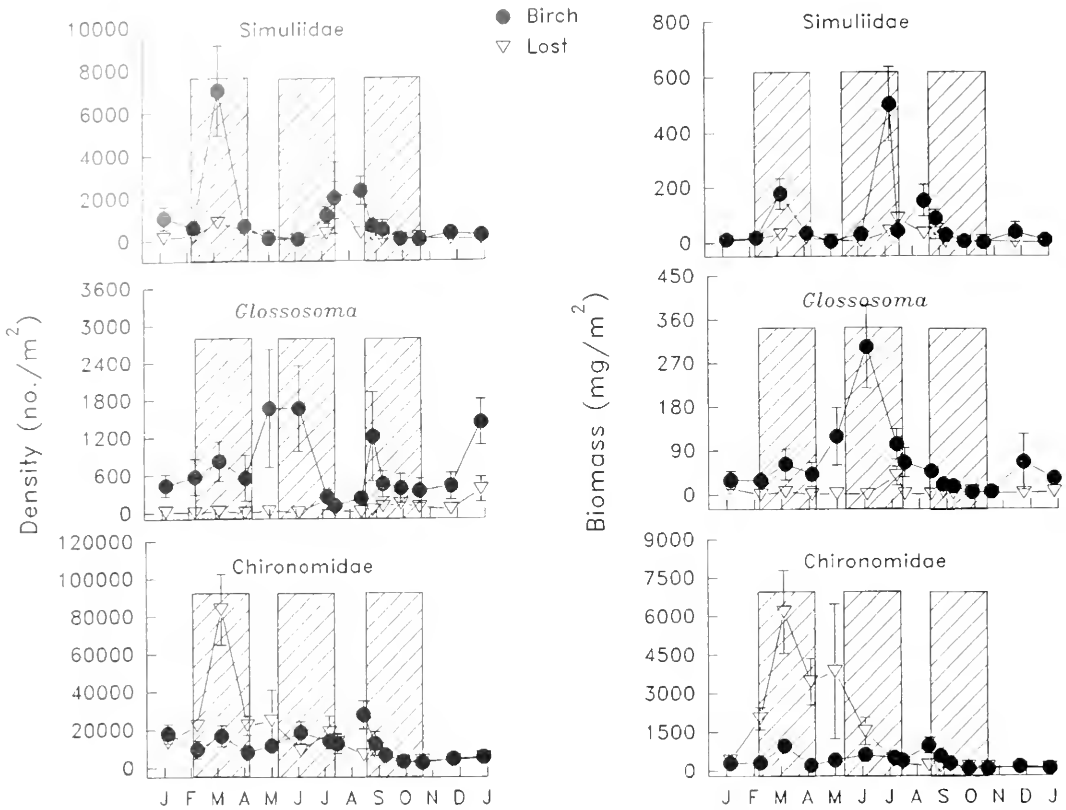

Fig. 3. Temporal patterns in benthic density and biomass for Simuliidae, *Glossosoma*, Chironomidae, *Baetis*, *Ephemerella*, and *Antocha*. Cross-hatched boxes represent periods when colonization experiments were conducted.

baseflow), experiment 2 from 14 May 1988 to 4 July 1988 ("spring" runoff), and experiment 3 from 25 August 1988 to 15 October 1988 ("summer" baseflow; Fig. 1). Macroinvertebrates were removed from all bricks on day 0 of each experiment using forceps to minimize disturbing algal standing crops on the bricks. Five randomly selected bricks were collected on each of days 1, 4, 9, 27, and 54. Day 4 bricks of experiment 2 could not be collected from Lost because of high flows.

Bricks were harvested by positioning a fine-meshed (250-μm) net immediately downstream of a brick and transferring the brick into the net. Individual bricks and net contents were put into storage bags, placed on ice, and returned to the laboratory. In the laboratory, macroinvertebrates were rinsed from bricks with a spray of water, preserved with 10% formalin, and processed as the benthic samples. Bricks then were frozen at −25°C for later algal biomass determinations.

Algal biomass was determined by immersing each brick in 100% reagent grade acetone for 24 h and analyzing the extractant for chlorophyll *a* using standard methods (APHA 1985). Next, all organic matter was scraped from each brick using a razor blade. This material was dried at 60°C, weighed, ashed at 550°C, rehydrated, redried at 60°C, and then reweighed for algal AFDM determination.

Macroinvertebrate data were expressed in terms of density, biomass, species richness, and Simpson's dominance index (Barbour et al. 1987). Density and biomass data also were calculated for the taxa noted above. Data were either transformed log(x+1) for abundance data or arcsine(sqrt(x)) for relative abundance data and analyzed for differences using the Kruskal-Wallis nonparametric test for each experiment (Zar 1984, Statsoft 1990). Plotted values are expressed as nontransformed means and standard deviations.

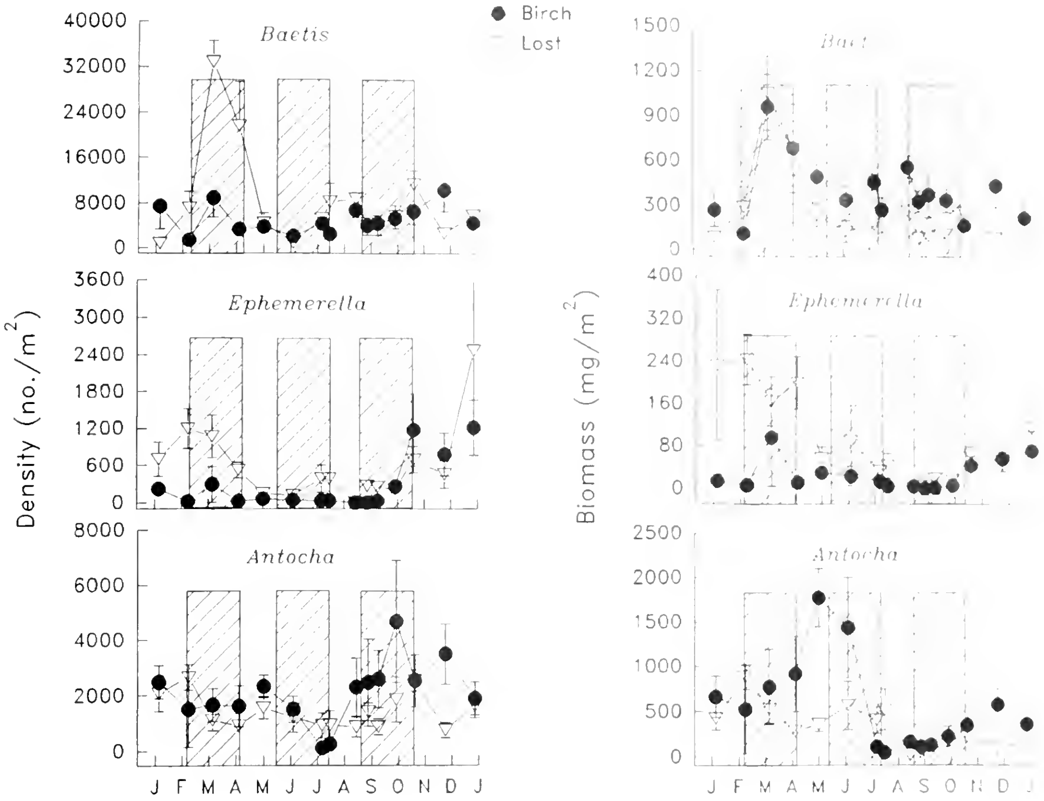

Fig. 3. Continued.

RESULTS

Temporal Trends in Benthic Macroinvertebrate Assemblages

Mean total density of macroinvertebrates was similar through time in Birch, whereas substantial seasonal fluctuations in abundance occurred in Lost (Fig. 2). Densities were greatest (ca. 3X) in March and lowest (ca. 0.3X) during spring runoff in Lost (Tukey's test, $p = .05$). Mean annual density was 32,600/m^2 (CV = .27) in Birch and 34,020/m^2 (CV = .76) in Lost. Mean biomass was substantially greater (ca. 2X), although nonsignificantly, in Birch than Lost for most of the year, except in late winter–early spring (Fig. 2). Mean annual biomass (dry-weight) was 5.62 g/m^2 (CV = .40) in Birch and 3.12 g/m2 (CV = .67) in Lost. Although more taxa were present in Lost on any given sampling date, mean species richness decreased by 10 taxa during spring runoff in Lost to below that found in Birch (Fig. 2).

Six taxa comprised a large proportion (>70%) of the benthic assemblage during the experiments: *Antocha*, *Baetis*, Chironomidae, *Ephemerella*, *Glossosoma*, and Simuliidae. These varied widely as to their relative abundance in each stream and during each experiment. For example, *Antocha* showed similar benthic densities during each experiment for both streams (Fig. 3), but its biomass was greater during winter and spring experiments than during the summer experiment, especially in Birch (Tukey's test, $p = .05$). *Baetis* displayed a substantial increase in benthic density during the winter experiment in Lost, but most of the time values were much lower and similar in both streams. Biomass of *Baetis* was greater in Birch than Lost, and biomass was greater during the winter experiment than the spring and summer experiments for both streams (Tukey's test, $p = .05$). Chironomidae were highly abundant during all colonization experiments, although significant increases in benthic density and biomass were found during

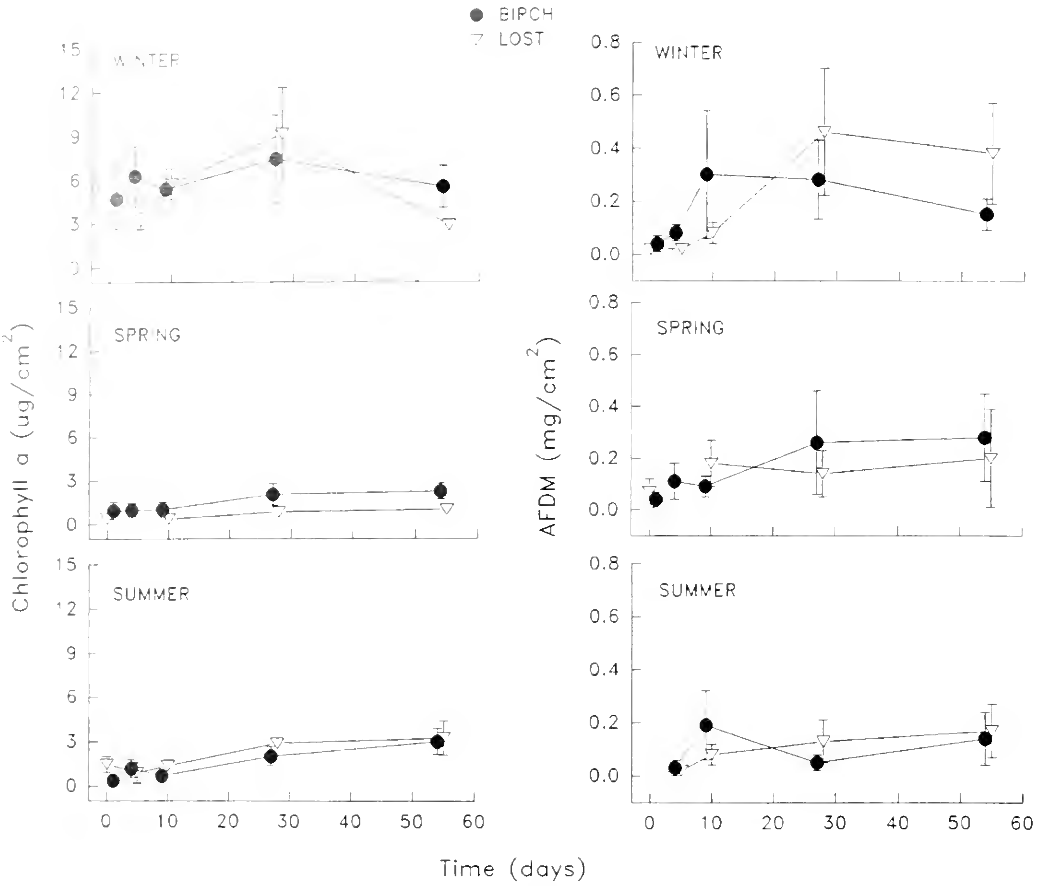

Fig. 4. Algal biomass as chlorophyll *a* and AFDM on bricks for each colonization experiment. *N* = 5 for each collection period. Bars represent +1 standard deviation about the mean.

the winter experiment in Lost (Tukey's test, *p* = .05).

Comparing all experiments in both locations, we found that benthic density and biomass of *Ephemerella* were greatest during the winter experiment in Lost (Tukey's test, *p* = .05, Fig. 3). *Glossosoma* always was more abundant in Birch than in Lost, with significant increases in benthic density and biomass occurring during the spring experiment in Birch (Tukey's test, *p* = .05). Simuliidae showed a significant increase in benthic density during the winter experiment in Birch (Tukey's test, *p* = .05). The benthic biomass of Simuliidae was greater during the winter and spring experiments than during the summer experiment in Birch (Tukey's test, *p* = .05). Simuliidae density and biomass were relatively low in [illegible] in Lost during all experiments.

Colonization Experiments

Periphyton biomass on the bricks was approximately 2–3X greater in the winter experiment for both streams than in the spring and summer experiments (Fig. 4). This higher biomass in winter was the result of a seasonal algal bloom of *Hydrurus foetidus* that occurred in both streams. Algal chlorophyll *a* levels increased over time (days 27 and 54) in Birch Creek during spring and summer (Tukey's test, *p* = .05). In general, algal AFDM levels remained unchanged during each experiment, except for periphyton AFDM during the winter experiment. No differences in AFDM levels were observed between streams during spring or summer experiments (Fig. 4).

Distinct seasonal patterns of macroinvertebrate colonization were found within and between streams and reflected seasonal

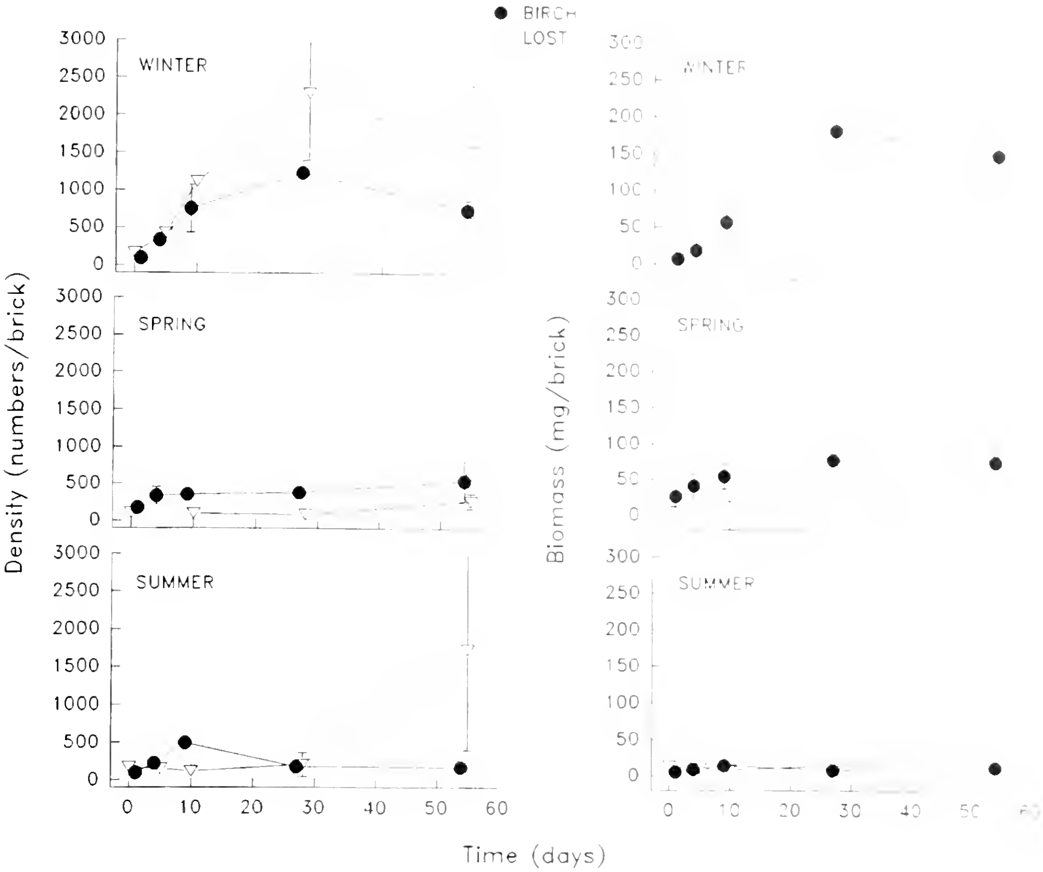

Fig. 5. Macroinvertebrate density and biomass on bricks for each colonization experiment. $N = 5$ for each collection event. Bars represent +1 standard deviation about the mean.

changes in benthic macroinvertebrate assemblages. For example, density and biomass of macroinvertebrates increased substantially and stabilized within 30 days of colonization during the winter experiment, with greater densities found in Lost (Tukey's test, $p = .05$; Fig. 5). These patterns reflect the greater benthic densities, especially in Lost, and biomass values during the winter experiment than during the other experiments (Fig. 2).

Colonization was inconsequential after day 1 in Lost during the spring experiment, reflecting low benthic density and biomass of macroinvertebrates in this stream during runoff (Fig. 5). Density and biomass during the spring experiment increased and plateaued by day 4 in Birch to values comparable to those at the end of the winter experiment.

During summer no distinct colonization pattern was evident for either stream, reflecting peaks in emergence and recruitment for many taxa in both streams (Robinson 1992). For example, density peaked in Birch by day 9 (Tukey's test, $p = .05$) but then dropped and remained low until the end of the experiment, whereas density remained low in Lost until a substantial increase on day 54 (Tukey's test, $p = .05$; Fig. 5). Biomass, on the other hand, remained low in both streams throughout colonization, suggesting the day 54 peak observed in Lost was due to an influx of early Chironomidae instars (see Fig. 3).

Species richness increased until day 27 during the winter experiment (Tukey's test, $p = .05$) in both streams, displaying patterns similar to density and biomass (Fig. 6). During spring, species richness peaked by day 9 in Birch (Tukey's test, $p = .05$) to levels observed in winter. Species richness remained unchanged in Lost at less than 10 taxa

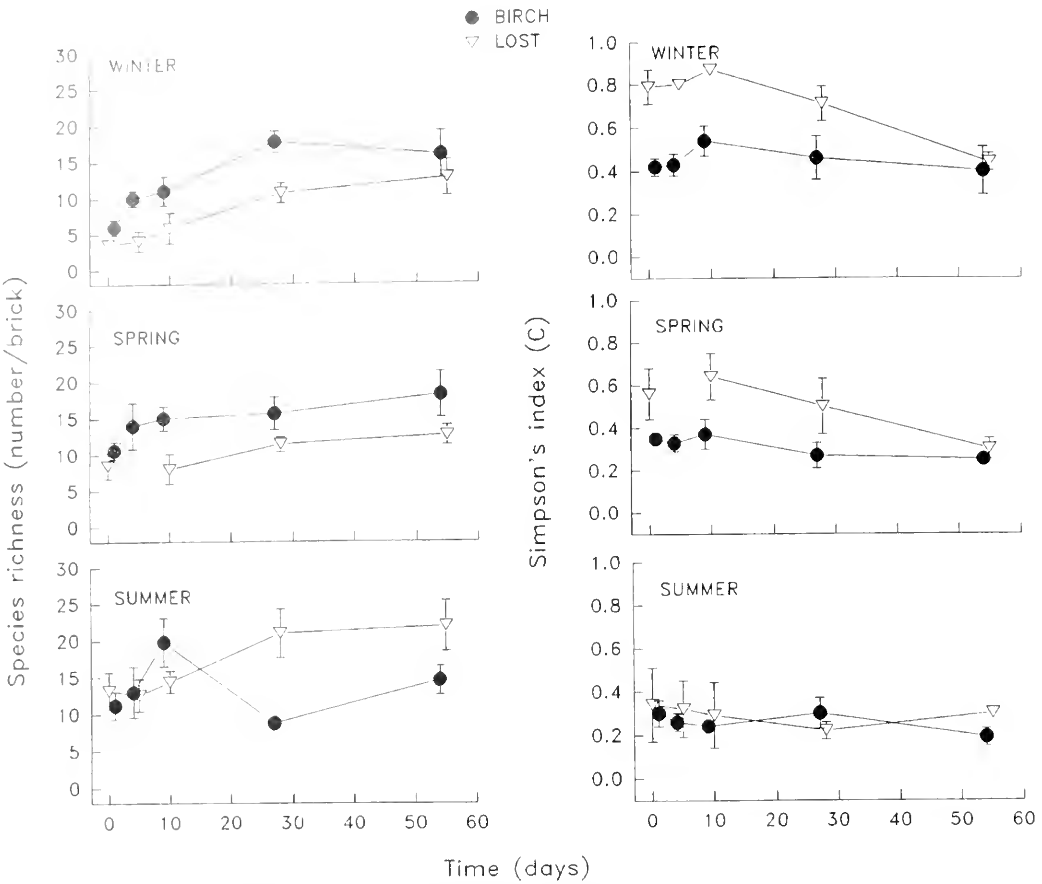

Fig. 6. Macroinvertebrate species richness and Simpson's index on bricks for each colonization experiment. $N = 5$ for each collection event. Bars represent +1 standard deviation about the mean.

throughout the experiment, similar to levels observed during the winter experiment. Species richness peaked by day 9 during summer in Birch and then decreased for the remainder of the experiment (Tukey's test, $p = .05$). Species richness in Lost displayed similar colonization patterns in summer as in the other seasons; however, species richness was about 2X as high in summer as in winter and spring (Fig. 6).

Simpson's index (C), an index of dominance, was substantially greater in Lost than in Birch during winter and spring experiments, except for day 54 (Tukey's test, $p = .05$; Fig. 6). Simpson's index was not significantly different among dates for each experiment in Birch, or streams and dates in the summer experiment ($p = .07$). Simpson's was highest during winter in both streams, reflecting the predominance of a few taxa (Table 1). For example, the Chironomidae comprised >70% of the assemblage in Lost during winter and spring experiments, but <70% during winter and <50% during spring and summer experiments in Birch. During winter *Baetis*, *Glossosoma*, and Simuliidae also were abundant in Birch, whereas only *Baetis* was abundant in Lost. During spring *Glossosoma* and Chironomidae were abundant in Birch, whereas Chironomidae and *Baetis* were predominant in Lost (Table 1). In summer the macroinvertebrate assemblages became more even (i.e., low Simpson's values). Here, *Baetis*, Chironomidae, *Glossosoma*, and Simuliidae were predominant in Birch, while *Antocha*, *Baetis*, and Chironomidae were abundant colonizers in Lost.

DISCUSSION

The process of colonization is complex and influenced by various factors. This study

TABLE 1. Mean (±SD) relative abundance (percent) of six selected macroinvertebrate taxa.

Taxon	Stream	Day 1	Day 4	Day 11	D[illegible] 2[illegible]	Day [illegible]
Experiment 1 (winter baseflow)						
Antocha	Birch	2(2)	1(1)	6(2)	6(2)	[illegible]
	Lost	0	0	0	0	0
Baetis	Birch	7(5)	10(3)	9(4)	10(3)	10(4)
	Lost	11(5)	10(2)	6(1)	11(5)	31(6)
Chironomidae	Birch	18(12)	62(5)	71(6)	66(10)	59(11)
	Lost	89(5)	89(2)	93(1)	81(8)	69(6)
Ephemerella	Birch	0	.4(.3)	3(2)	1(2)	1(1)
	Lost	0	4(.5)	2(2)	2(2)	2(2)
Glossosoma	Birch	33(21)	6(3)	5(5)	8(4)	12(5)
	Lost	0	0	0	0	0
Simuliidae	Birch	7(7)	19(7)	11(4)	11(8)	1(6)
	Lost	0	0	2(2)	0	7(1)
Experiment 2 (spring runoff)						
Antocha	Birch	0(0)	0(0)	3(2)	3(3)	0(0)
	Lost	1(2)	na	2(2)	1(1)	0(0)
Baetis	Birch	7(2)	6(2)	5(1)	8(1)	6(5)
	Lost	11(6)	na	4(5)	11(5)	25(6)
Chironomidae	Birch	51(1)	42(7)	40(17)	41(9)	45([illegible])
	Lost	71(9)	na	78(8)	68(15)	46(8)
Ephemerella	Birch	1(1)	1(.4)	5(.3)	6(8)	0(0)
	Lost	1(1)	na	5(1)	1(2)	4(1)
Glossosoma	Birch	26(6)	38(9)	38(13)	25(4)	10(4)
	Lost	1(2)	na	1(1)	0(0)	0(0)
Simuliidae	Birch	2(2)	0(0)	16(6)	5(4)	16(4)
	Lost	3(3)	na	1(1)	2(1)	10(5)
Experiment 3 (summer baseflow)						
Antocha	Birch	4(4)	1(1)	2(1)	2(1)	4(1)
	Lost	17(10)	9(8)	9(7)	12(6)	8(7)
Baetis	Birch	17(9)	16(6)	20(2)	19(5)	25(4)
	Lost	44(21)	44(19)	28(19)	25(8)	35(10)
Chironomidae	Birch	43(11)	38(8)	42(4)	45(11)	25([illegible])
	Lost	20(11)	27(10)	34(20)	27(12)	35(15)
Ephemerella	Birch	.3(.5)	.1(.3)	3(1)	0(0)	0(0)
	Lost	2(1)	1(1)	5(2)	1(2)	1(1)
Glossosoma	Birch	8(11)	13(9)	9(4)	20(16)	18(10)
	Lost	.1(.3)	1(1)	8(5)	18(9)	1(1)
Simuliidae	Birch	14(5)	13(17)	5(2)	6(5)	1(2)
	Lost	.3(.6)	0(0)	0(0)	0(0)	2(2)

addressed the role of season and flow regime on colonization dynamics. Little Lost River is comprised of primarily more mobile r-adapted taxa, while Birch Creek has a predominance of relatively sessile K-adapted taxa (Robinson 1992). Consequently, one would expect colonization to be more rapid in Lost across seasons (Mackay 1992). However, benthic density of organisms also plays an important role, with colonization being more rapid at times of high benthic density (Shaw and Minshall 1980, Ciborowski and Clifford 1984, Benson and Pearson 1987, Robinson et al. 1990). In this study benthic density and biomass of organisms were substantially greater during the winter experiment, and benthic density was greater in Lost than in Birch. Similarly, colonization densities were greater in both streams in winter than in spring and summer, and abundance of organisms on the bricks was greater in Lost than in Birch. However, colonization required about 30 days in winter for both streams, but less than 10 days in spring and summer. This supports the idea that water temperature directly influences colonization rates by enhancing macroinvertebrate activity during periods of warm temperature, as found by Doeg et al. (1989) and Mackay (1992).

Life history characteristics of a stream assemblage are one of the more important factors influencing colonization at the scale of individual streams. Life history attributes are a function of interaction between environment and respective genotypes (Tauber et al. 1986), of which flow regime is an important selective mechanism of lotic environments (Poff and Ward 1989) by dictating the kinds of organisms present in a stream (Minshall 1988). Spring runoff provides a major abiotic constraint (i.e., a disturbance event; Poff 1992) on community structure and populations in Lost that is not present in Birch as shown by the reduction in mean benthic density and species richness. Indeed, colonization essentially was absent in Lost during spring runoff, with colonizer density and biomass being 2–10X greater in Birch. Chironomidae and *Baetis* were predominant on bricks in Lost, whereas *Glossosoma*, a relatively sessile taxon, was predominant in Birch during spring (Table 1). Kohler (1992) found that *Glossosoma* was a strong competitor by physically interferring with a number of taxa. His study stream also had a relatively constant flow regime as found in Birch. Similarly, Diamond and Reice (1985) found that initial colonists can influence colonization by some taxa. *Glossosoma*, being an initial colonizer, may impose a biotic constraint (competition) on colonization in Birch during spring. Furthermore, in North American temperate streams, environmental conditions are optimal for reproduction of many aquatic insects in summer (Benke 1984). For example, Clifford (1978) found that summer months were the primary reproduction period in a Canadian brownwater stream. Robinson et al. (1990) also found summer months to be the most active period for aquatic insects in Mink Creek, located in southeast Idaho. Peak emergence and recruitment also occurred in Birch and Lost during the summer baseflow period (Robinson 1992). Benthic density and biomass were lower during the summer experiment, with colonization reflecting the benthic condition. Assemblages on bricks also appeared more evenly distributed, as shown by lower Simpson's values. These data demonstrate that seasonal changes in assemblage structure directly influence colonization.

Data also indicate major seasonal differences in community structure within and between streams. A number of other studies have shown that the impact of physical disturbance on benthic communities differs among seasons, reflecting differences in animal abundance (Robinson and Minshall 1986, Robinson et al. 1990), and among streams with different flow regimes (e.g., see references in Minshall 1988, Poff and Ward 1989, Mackay 1992). Our study suggests that a natural disturbance event would have a pronounced impact during winter in both streams when animal density and biomass are high, but little impact during late summer when many populations have emerged (see also Wallace 1990). Robinson et al. (1990) found an influence by disturbance in fall but not in summer in an Intermountain stream. However, one would expect little impact from physical disturbance in Lost in spring because organisms should have evolved morphologies and/or life history strategies to the harsh spring runoff conditions. In contrast, physical disturbance should have a greater impact in Birch because organisms have adapted to the seasonally constant flow regime.

In summary, a variety of colonization patterns were observed between these streams among the three seasons of study. Our data suggest that colonization differs seasonally among streams, reflecting differences in general life history characteristics and benthic densities of macroinvertebrate communities. These seasonal differences in colonization are attributed to differences in flow regime, its interaction with lotic thermal properties, and their consequent influence on community structure and population dynamics. Apparently, spring runoff is a considerable abiotic constraint on populations in Lost, with colonization being greatly reduced at this time because aquatic insects are absent due to life history or present elsewhere in refugia. In contrast, Birch maintains a constant flow regime, and colonization in spring follows the pattern observed during winter for both streams. The reduced colonization in Birch, in terms of biomass, during spring may result from life history, e.g., presence of early instars, and/or competition. Colonization is a complex interplay between community properties and life history adaptations resulting from different physical environments (geomorphology) among streams, such as differences in flow regime and temperature.

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NONSTRUCTURAL CARBOHYDRATE AND ELEMENT POOLS IN GLOBEMALLOW (*SPHAERALCEA*): DEFOLIATION EFFECTS AND SEASONAL TRENDS

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and Philip A. Harrison[1]

ABSTRACT.—Globemallows (*Sphaeralcea* spp.) are arid land forbs suitable for seeding with crested wheatgrass (*Agropyron cristatum* [L.] Gaertner). However, little is known about the quantitative role of total nonstructural carbohydrates (TNC) in relation to globemallow tolerance of grazing, or about seasonal dynamics of mineral elements. The objectives of this study were to compare TNC and element pools (concentration × biomass) in the roots, crowns, and shoots of clipped versus unclipped *S. munroana* (Dougl.) Spach. Seedlings of *S. munroana* were transplanted to a northern Utah field site in 1985. Interplanted crested wheatgrass provided a uniform competitive background. One-half of the globemallows were clipped to 5 cm on 10 May 1986 when stems were elongating and root and crown TNC pools were low. The remaining globemallows were not clipped. Root, crown, and shoot pools of TNC and elements (N, P, K, Ca, and Mg) were determined on 1 May, 20 May, 7 June, 11 July, 22 September, and 5 November 1986, and 29 May 1987. Defoliation did not affect shoot weights during a 1-year period. Experiment-long TNC and element pools also were not affected by clipping. Results indicate that *S. munroana* shoot recovery from a single spring grazing during a 1-year period would not be impaired by low root and crown TNC pools, and that TNC stored in the roots and crowns would account for only 7% of the regrowth produced. Furthermore, TNC and element pools of roots and crowns were generally constant from May to September but increased from September to November. TNC and element pools in shoots increased from May to September and then generally declined by November. TNC pools of roots and crowns declined during winter.

Key words: Sphaeralcea munroana, *clipping effects, herbivory, animal nutrition.*

Globemallows (Malvaceae: *Sphaeralcea*) are perennial forbs native to the western USA and are of interest for rangeland seeding (Horton 1989, Pendery and Rumbaugh 1990). Several studies have shown that globemallows are grazed by livestock and wildlife (Hyder et al. 1975, Howard et al. 1990, Rumbaugh et al. 1993a). Understanding factors related to globemallow tolerance to grazing would enhance our ability to manage these species.

Total nonstructural carbohydrates (TNC) in roots and crowns have been considered an important energy source for the regrowth of grass and forb shoots following defoliation (Brown et al. 1972, Holechek et al. 1989). However, research by Caldwell et al. (1981) and Richards and Caldwell (1985) showed that root and crown TNC concentrations or pools (concentration × biomass) were not strongly correlated with the regrowth of defoliated *Agropyron* bunchgrasses. Recent work with alfalfa has also questioned the role of root TNC in shoot regrowth (Fankhauser and Volenec 1989, Hendershot and Volenec 1989).

Studies in Colorado investigated herbivory tolerance of *S. coccinea* (Nutt.) Rydb. in relation to root and crown TNC concentrations (Trlica et al. 1977, Menke and Trlica 1983). Herbivory tolerance of globemallow has not been investigated in relation to TNC pools. Furthermore, mechanistic studies such as the etiolated regrowth technique (Richards and Caldwell 1985) have not been done to evaluate the degree to which stored TNC contribute to the regrowth of globemallows following defoliation. While TNC have been the focus of many herbivory tolerance studies, elements may also be associated with herbivory tolerance (Chapin 1980a, 1980b, Chapin et al. 1980, Caldwell et al. 1981).

Seasonal trends of TNC concentrations in *S. coccinea* were studied by Menke and Trlica (1981). Rumbaugh et al. (1993b) reported element concentrations in globemallow taxa in

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the spring and fall. However, seasonal trends of element and TNC pools in globemallow have not been reported.

The first objective of this study was to determine if pools of TNC and elements (N, P, K, Ca, Mg) in the roots, crowns, and shoots of clipped versus unclipped *S. munroana* differed on seven dates over a 1-year period. The second objective was to determine the amount of regrowth produced in light versus dark by *S. munroana* clipped during the stems elongating or the seed shattering phenological stages.

MATERIALS AND METHODS

Study Site and Experimental Planting

These studies were conducted 3 km south of Logan, Utah (41°45'N, 111°48'W, 1389 m) in 1986 and spring 1987. Mean annual precipitation and temperature based on 28 years of records from a recording station 2 km from the study site were 471 mm and 7.4°C, respectively. Total precipitation and average temperature were 718 mm and 8.3°C in 1986, and 426 mm and 7.7°C in 1987. Soil at the site is a Nibley silt clay loam (Aquic Arginstoll).

Seeds of *S. munroana* were purchased commercially. The collection site was near Vernal, Utah, in pinyon-juniper (*Pinus-Juniperus*) vegetation on a sandy soil. Globemallow seeds were germinated and the seedlings transplanted into containers (164 cm^3) containing a rooting medium of 4 parts sand: 2 parts peat moss: 1 part vermiculite. Plants were grown with no fertilization in the greenhouse during the winter of 1985. Crested wheatgrass seeds also were purchased commercially, and the plants were grown in the greenhouse as described above.

Crested wheatgrass and globemallow plants were transplanted to the field on 1 May 1985. They were planted in a checkerboard pattern with 0.5-m spacing between plants. Therefore, each plot was 1 × 1 m, with four crested wheatgrasses competitors surrounding each *S. munroana*. The planting was 33 × 7 m overall.

TNC and Element Study

This study had a completely randomized experimental design with two treatments (clipped versus unclipped plants) and seven sampling dates. Twelve previously unclipped *S. munroana* plants were sampled for TNC and elements on 1 May 1986 when most plants were in the leaves elongating phenological stage (phenological terminology follows Menke and Trlica [1981]). Seventy-two other globemallow plants were assigned to be clipped or unclipped. Clipping was done at a 5-cm height on 10 May 1986 when stems were elongating.

Six clipped and six unclipped globemallow plants were then sampled on 20 May, 7 June, 11 July, 22 September, and 5 November 1986, and 29 May 1987. The most common phenological stages on these dates were stems elongating, flower buds developing, fruit developing, leaves brown, fall quiescence, and flower buds developing, respectively. These stages represented most of the phenological conditions occurring during a growing season. Furthermore, root and crown TNC concentrations in *S. coccinea* are lowest during the stems elongating phenological stage (Menke and Trlica 1981). Assuming similar patterns for TNC pools in *S. munroana*, we expected clipping at this stage to have its greatest impact on the reestablishment of shoots, if the quantity (pool) of soluble carbon in roots and crowns is important for recovery. Crested wheatgrass plants also were clipped to 5 cm on 10 May 1986 because crested wheatgrass stands often are grazed in the spring (Horton 1989).

Plants of *S. munroana* were sampled between 0800 and 1200 h to minimize the effects of diurnal fluctuations in TNC (Chatterton et al. 1972). Sampled plants were divided into roots, crowns, and shoots. Crowns included about 1.5 cm of root and stem. Following excavation of soil monoliths (30 × 30 × 30 cm) the shallow braided tap roots were carefully separated from the soil with hand tools. This method sampled only a portion of the root system because roots extended to a greater depth and radius than the soil monolith; however, it was a practical attempt to extract roots given limited resources. Likewise, small fine roots within the soil monolith were probably only partially sampled. These shortcomings mean that root pools were underestimated. Plant parts were washed in a series of three water-filled plastic tubs in the field and placed in a portable freezer (−7 C). Samples were transferred to another freezer (−18 C) at the end of the day, where they were stored prior to chemical analyses.

Fifty-milligram subsamples of ground, lyophilized plant tissue were analyzed for TNC, as described by Chatterton et al. (1987). A commercial amylase preparation was used to digest starch in the tissue (0.1% Clarase 40,000 for 24 h at 38°C). TNC were determined colorimetrically and included starch and soluble carbohydrates. Plant weights were evaluated on a structural dry-weight basis, which is the plant part dry weight minus TNC. This method avoids errors associated with simultaneous changes in carbohydrate content and dry weight (Chatterton et al. 1987).

Additional 0.5-g subsamples of the plant tissue were digested in 3:1 nitric:perchloric acid, diluted (1:100) with water, and analyzed colorimetrically for P using the vanadomolybdate procedure (Greweling 1976). A second aliquot was further diluted (1:10) with 1 g La L^{-1} as $LaCl_2$ and analyzed for Ca and Mg by atomic absorption spectrometry, and for K by flame emission spectrometry (Greweling 1976). Total N was determined by the Kjeldahl procedure (Bremner 1965). The 29 May 1987 samples were inadvertently discarded before elemental analyses were done.

Etiolated Regrowth Study

This study was a 2 × 2 factorial in a completely randomized experimental design. Twenty globemallow plants were clipped on 11 May 1986 when the stems were elongating. Ten of these plants were covered with plastic buckets painted black on the inside and white on the outside. The other 10 plants were not covered and regrew under ambient light conditions. Twenty other globemallow plants were clipped on 21 July 1986 during seed shattering when growth was much slower, and when we expected TNC pools in the roots and crowns to be higher than in the spring. Again 10 plants were covered with buckets and the other 10 were not covered. All plants were harvested when etiolated regrowth was not apparent for 1 week, which was on 31 May and 25 August for plants clipped in the stems elongating and seed shattering stages, respectively. Harvested material was dried (60°C) and weighed. Because plants of *S. munroana* were selected from the experimental planting border in this study, they had three crested wheatgrass competitors, not four as in the previous study.

Statistical Analyses

Data were reduced and analyzed by analysis of variance with SAS (SAS Institute, Inc. 1985). Clipping was considered a fixed factor, and date of sampling was considered a random factor in the TNC and element study. Phenological stage and regrowth environment (light or dark) were considered fixed factors in the etiolated regrowth study. Single degree of freedom contrasts and protected least significant difference tests were used to determine

Table 1. Average effects of clipping on 10 May 1986 versus not clipping on seven response variable pools measured for globemallow roots, crowns, and shoots. Clipped versus unclipped plant means did not differ significantly for any response variable ($P > .05$; $n = 36$ for TNC and weight responses, otherwise $n = 30$). Whole-plant pools (the sum of root, crown, and shoot pools) also did not differ significantly due to clipping for any response variable.

Clipping treatment	TNC[a]			Weight			N		
	Root	Crown	Shoot	Root	Crown	Shoot	Root	Crown	Shoot
	mg			g SDW[b]			mg		
Clipped	1000	372	2163	10	8	28	64	51	232
Unclipped	995	179	2118	11	8	28	106	72	330

	P			K			Ca			Mg		
	Root	Crown	Shoot	Root	Crown	Shoot	Root	Crown	Shoot	Root	Crown	Shoot
	mg											
Clipped	13	9	16	112	83	145	176	115	414	35	25	117
Unclipped	17	10	51	115	95	173	191	116	433	34	25	109

[a]TNC = total nonstructural carbohydrate

[b]SDW = structural dry weight (see Materials and Methods)

which means differed significantly. Differences were considered significant for all test statistics when $P \leq .05$.

RESULTS

Interactions between clipping treatment and sampling date were not statistically significant for TNC or element data. Moreover, clipping did not significantly affect experiment-long mean TNC, N, P, K, Ca, or Mg pools (Table 1). When averaged over all sampling dates, plant part weights (roots, crowns, shoots, or whole plants) also were not significantly affected by clipping.

The phenological stage by regrowth environment interaction was not significant in the statistical analyses of the etiolated regrowth data. However, *S. munroana* plants regrowing in the light produced significantly more shoot regrowth than plants regrowing in the dark (Fig. 1). The amount of regrowth did not differ significantly between the stems elongating and seed shattering stages.

Root TNC pools increased significantly between 7 June and 22 September, and between 22 September and 5 November (Fig. 2). Root TNC pools declined significantly during winter. Crown TNC pools were statistically constant until 22 September, increased significantly between 22 September and 5 November, and then declined significantly during winter. Shoot TNC pools tended to increase during the growing season, although this trend was not significant until 22 September. Unlike crowns and roots, shoot TNC pools declined significantly between 22 September and 5 November. Whole-plant TNC pools increased significantly between 1 May and 22 September, remained at a high level through 5 November, and then declined

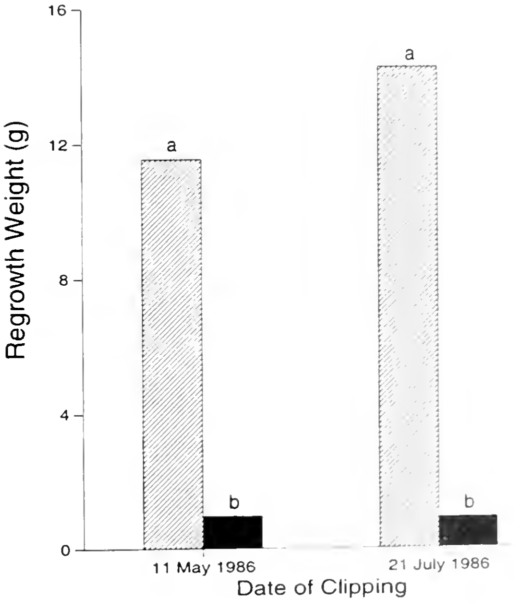

Fig. 1. Mean regrowth biomass of plants initially clipped 11 May and 21 July 1986 and regrown in sunlight (crosshatched bars) or in the dark (black bars) for 20 and 27 days, respectively. Plants were in the stems elongating and seed shattering phenological stages on 11 May and 21 July, respectively. Means with different letters differed significantly ($P \leq .05$, $n = 10$).

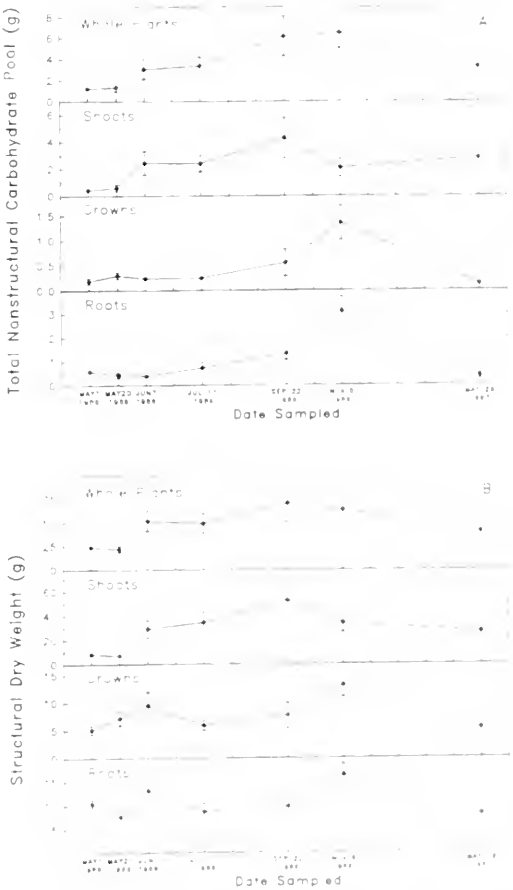

Fig. 2. Total nonstructural carbohydrate [illegible] (A) and structural dry weights (B) of [illegible] shoots, and whole plants [illegible] 1986 [illegible]. Means ± 1 standard error are [illegible] unclipped plants ($n = 12$). Structural [illegible] calculated by subtracting the total nonstructural carbohydrate pool from the plant part dry weight.

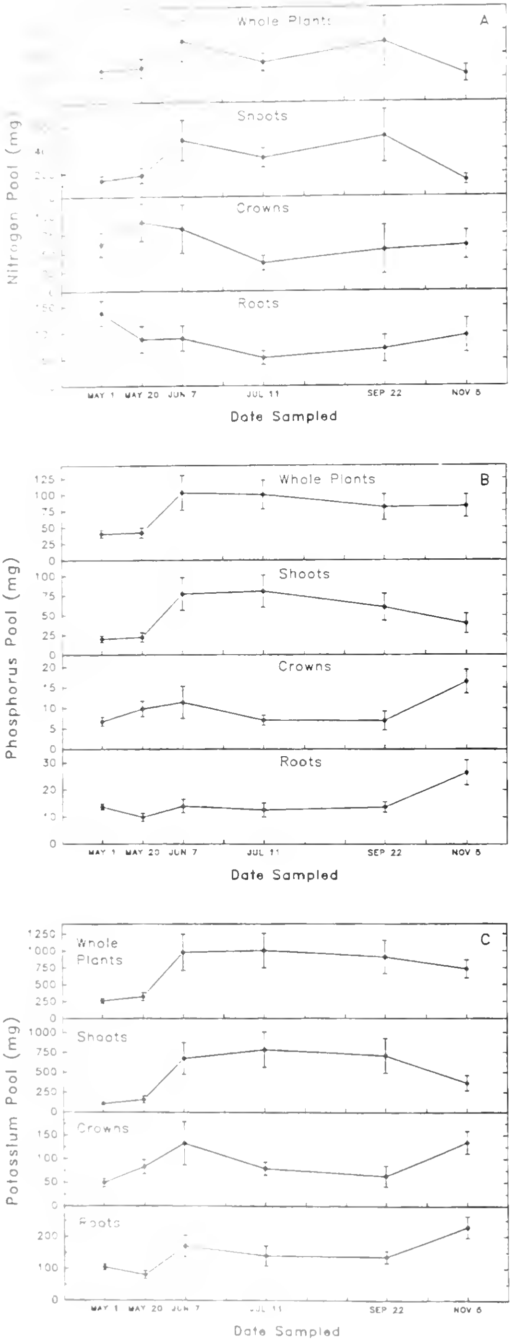

Fig. 3. Nitrogen (A), phosphorus (B), and potassium (C) pools in globemallow roots, crowns, shoots, and whole plants on six sampling dates in 1986. Means (±1 standard error) are the average of clipped and unclipped plants (n = 12).

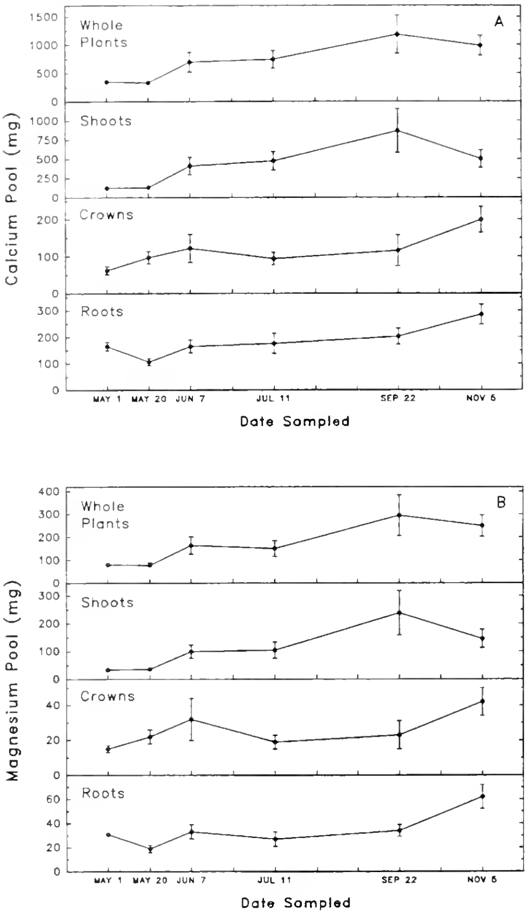

Fig. 4. Calcium (A) and magnesium (B) pools in globemallow roots, crowns, shoots, and whole plants on six sampling dates in 1986. Means (±1 standard error) are the average of clipped and unclipped plants (n = 12).

significantly during winter. Shoots contained the largest proportion of the TNC pool from 7 June to 22 September. Crowns and roots together were a relatively large soluble carbon pool on 1 May, 20 May, and 5 November.

Significant differences in element pools also were found on different dates (Figs. 3, 4). Root and crown pools were statistically constant between 1 May and 22 September, with the exception of root N pools. Root and crown P, K, Ca, and Mg pools increased significantly between 22 September and 5 November. Shoot element pools increased significantly between 1 May and 22 September. Shoot pools tended to decline from their seasonal highs by 5 November (significantly for N and P, nonsignificantly for K, Ca, and Mg).

DISCUSSION

Clipping Effects

The experimental planting and clipping treatment in our study simulated a crested wheatgrass stand interseeded with forbs in which all species are heavily grazed once annually, as in some rotational grazing systems. Our results indicated that a single grazing during the stems elongating phenological stage would not significantly affect average shoot weights of *S. munroana* during a 1-year period (Table 1). If low root and crown TNC pools in early May (Fig. 2) impair shoot recovery following a single spring grazing event, differences in clipped versus unclipped plant shoot weights should have occurred. While stored TNC were not important for long-term regrowth in this study, stored TNC may have contributed to short-term (1–7 days) recovery (Smith and Silva 1969, Richards and Caldwell 1985). Also, results might have differed had clipping been done at other phenological stages; however, this study was not designed to examine those questions.

Our results also showed that TNC in roots and crowns accounted for only 7% of the biomass in regrowing shoots following clipping during the stems elongating and seed shattering phenological stages (Fig. 1). We assume the remainder of the regrowth was derived from TNC produced by current photosynthesis. While root and crown TNC pools were not quantitatively large contributors to shoot regrowth, Richards and Caldwell (1985) pointed out that the efficiency with which a species allocates available carbon to aboveground meristems and utilizes the carbon for new foliage may be a key physiological feature determining the species' ability to tolerate defoliation by large grazing animals. We did not address meristematic limitations or the efficiency of TNC allocation to shoot regrowth in *S. munroana*.

While a 5-cm clipping height is frequently used in clipping studies (e.g., Richards and Caldwell 1985), it may be more severe than most grazing. Spring grazing by sheep in Utah caused most forbs to be defoliated once or twice and reduced the leaf area index by 55% (Hodgkinson 1980). Rumbaugh et al. (1993a) reported 75% utilization of globemallows grazed by sheep in small experimental pastures during the spring. We estimate our clipping treatment reduced leaf area about 90%. Moreover, if the plant community or herbivory pattern were more complex, interspecific and intraspecific differences in carbon accumulation and translocation efficiency could occur, which might affect responses to grazing and the competitive balance among species.

Trlica et al. (1977) found that *S. coccinea* plants clipped once during early or rapid growth had root and crown TNC concentrations that did not differ significantly from unclipped plants after 14 or 26 months. Menke and Trlica (1983) reported that *S. coccinea* plants clipped once at any of five phenological stages did not have significantly different root and crown TNC concentrations relative to control plants. They also found that TNC concentrations were reduced only when repeated clippings were applied.

Seasonal Trends

Root and crown TNC pools in *S. munroana* were relatively low through much of the growing season but exhibited a sharp increase in the fall (Fig. 2), which is similar to the trends for TNC concentrations for *S. coccinea* reported by Menke and Trlica (1981). However, Menke and Trlica (1981) predicted that species with "flat" or "extended" root and crown TNC cycles would be sensitive to defoliation unless they are rhizomatous, like *S. coccinea*. *S. munroana*, which had flat root and crown TNC cycles (Fig. 2), but which is not rhizomatous, was not significantly affected by a single severe defoliation (Table 1). The significant decline in shoot TNC pools between 22 September and 5 November and the concomitant increase in root and shoot pools, probably reflected senescence and translocation of TNC to the roots and crowns for wintertime respiration.

Large increases in shoot element pools from mid-spring through summer (1 May–22 September), coincident with statistically constant root plus crown pools, indicated that elements were being absorbed from the soil or from portions of the root system not sampled (Figs. 3, 4). Increases in root plus crown pools during the fall (22 September–5 November) could have been met by translocation from senescing shoots, which had decreasing element pools during the fall. Chapin (1980b) and Chapin et al. (1980) reported that perennial

TABLE 2. Concentrations of total nonstructural carbohydrates (TNC) and five elements in globemallow shoots on seven sampling dates in Cache Valley, Utah. Means (±1 standard error) are the average of clipped and unclipped plants (n = 12).

Constituent	1 May 1986	20 May 1986	1 June 1986	11 July 1986	22 Sept. 1986	5 Nov. 1986	29 May 1987
	mg g^{-1a}						
TNC	52.5 ± 6.3	62.5 ± 11.0	72.8 ± 7.6	74.4 ± 7.2	84.2 ± 5.4	58.5 ± 5.8	115.7 ± 8.5
N	19.1 ± 3.6	15.2 ± 3.3	16.5 ± 3.5	11.6 ± 2.1	7.8 ± 2.1	6.4 ± 2.0	—
P	2.6 ± 0.3	2.3 ± 0.2	2.6 ± 0.1	2.2 ± 0.1	1.1 ± 0.1	1.1 ± 0.1	—
K	11.4 ± 0.9	15.5 ± 1.3	21.2 ± 0.8	20.1 ± 0.5	13.0 ± 0.7	10.3 ± 0.6	—
Ca	14.1 ± 0.6	13.9 ± 0.9	13.5 ± 0.7	12.8 ± 0.5	17.0 ± 1.1	14.8 ± 0.8	—
Mg	4.1 ± 0.2	3.9 ± 0.2	3.4 ± 0.2	2.7 ± 0.1	4.1 ± 0.1	4.3 ± 0.3	—

[a] TNC concentrations are on a structural dry weight basis (see Materials and Methods).

plants of infertile habitats support spring growth more by drawing on stored nutrients than by concurrent absorption from the soil. Depleted nutrient reserves are gradually replenished during the summer by absorption from the soil and during the autumn by translocation from senescing leaves.

Element levels expressed as concentrations are useful for consideration of the nutritional value of S. *munroana* shoots to herbivores (Table 2). For cow-calf livestock operations these nutrient concentrations are likely low to adequate (Church 1988). Rumbaugh et al. (1993b) found that swards of crested wheatgrass and globemallow were nutritionally adequate for livestock in spring and fall. The accession of S. *munroana* used in this study was also studied by Rumbaugh et al. (1993b), and they found somewhat higher N, P, K, Ca, and Mg concentrations in this accession at their Idaho study site than we did at our Utah study site.

Shoot N, P, and K concentrations were highest in the spring and lowest in the fall (Table 2). Shoot TNC concentrations tended to be higher in the summer and fall than in the spring. Chapin et al. (1986) found that tundra herbivores selected plants with high N, P, and K concentrations during early growth but generally did not select plants high in leaf TNC. They interpreted this as indicating nutrients were more important than energy in summer forage selection. Rumbaugh et al. (1993a) found that consumption of globemallows (including the accession of S. *munroana* used in this study) by sheep was significantly higher in the spring than in the fall, and Rumbaugh et al. (1993b) reported that utilization appeared to be positively influenced by leaf N concentrations and stem Ca:P ratio.

Chapin et al. (1986) found that N, P, and K concentrations were positively correlated with each other in leaves. They found that TNC concentrations were weakly and negatively correlated with N, P, and K concentrations. We found significant positive correlations among N, P, and K concentrations in shoots (Table 3). Concentrations of N and P were not significantly correlated with TNC concentration; however, K had a significant positive correlation with TNC.

SUMMARY AND CONCLUSIONS

A single, severe spring clipping when root and crown TNC pools were low did not significantly affect the average shoot weight of S. *munroana* through a 1-year period. Experiment-long TNC, N, P, K, Ca, and Mg pools in the roots, crowns, shoots, and whole plants of S. *munroana* also were not significantly affected by clipping. The etiolated regrowth experiment showed that TNC in roots and crowns accounted for only 7% of the shoot biomass in globemallow regrowing after clipping. These results indicate that S. *munroana* shoot recovery from a single spring grazing through a 1-year period would not be impaired by low root and crown TNC pools, and that TNC in

TABLE 3. Pearson correlation coefficients (*r*) among globemallow shoot weight, total nonstructural carbohydrate (TNC) concentration, and five element concentrations.

	TNC	N	P	K	Ca	Mg
Wt.	.18	–.23	–.34**	.02	–.17	–.11
TNC	—	.10	–.09	.25*	.14	–.20
N		—	.60**	.29*	.16	.09
P			—	.49**	–.09	–.03
K				—	–.08	–.44**
Ca					—	.42**
Mg						—

*$P \leq .05$
**$P \geq .01$

the roots and crowns would not make a quantitatively large contribution to regrowth. TNC and element pools of roots and crowns were generally constant from May to September but increased from September to November. TNC and element pools in shoots increased from May to September and then generally declined by November. TNC pools of roots and crowns declined during winter.

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TEMPORAL AND SPATIAL PATTERNS OF SMALL MAMMAL DENSITY AND SPECIES COMPOSITION ON A RADIOACTIVE WASTE DISPOSAL AREA: THE ROLE OF EDGE HABITAT

John D. Boone[1] and Barry L. Keller[2]

ABSTRACT.—Small mammal populations inhabiting radioactive waste disposal areas could be important vectors of contaminant redistribution, given sufficiently high numbers. Earlier studies conducted at the Subsurface Disposal Area (SDA) in southeastern Idaho found small mammal densities equaling or exceeding densities in native habitat. Our live-trapping study was conducted in 1988 and 1989 to assess the role of edge habitat (where SDA crested wheatgrass [*Agropyron cristatum*] plantings and native sagebrush habitat are separated by an earthen dike) in facilitating use of this highly modified site by small mammals. Small mammals had a significantly greater density in SDA edge habitat than in the interior. Total density of small mammals on and immediately around the SDA appeared to be less variable over time than density in native sagebrush habitat for years when data were available. This phenomenon was largely attributable to steady or increasing SDA population densities of the most common species, *Peromyscus maniculatus* and *Perognathus parvus*, during 1988–89, when most small mammal species had below-average densities in surrounding areas. The variety of foraging options in edge habitat may have allowed these relatively opportunistic species to avoid widespread population declines associated with drought years in 1988–89. Movements by *P. maniculatus* across the boundary were common, suggesting that this species did indeed utilize both habitat types. Preferences for edge habitat could potentially be used to formulate strategies that reduce use of the waste site by small mammals.

Key words: radioactive waste, small mammals, edge habitat, movements, Peromyscus maniculatus, *crested wheatgrass.*

Although artificially irradiated animals have been the subject of numerous investigations (Bongiorno and Pearson 1964, French and Kaaz 1968, Turner and Lannom 1968), interest in wildlife populations inhabiting radioactive waste disposal areas has been comparatively limited (Dunaway and Kaye 1961, Markham et al. 1978, Hedlund and Rogers 1980, Filipovich 1983, Groves and Keller 1983, Arthur et al. 1986, Groves et al. 1986). Knowledge of interactions of wildlife with stored radioactive waste is, however, essential for controlling biological assimilation and transport of contamination, and for maintaining waste stabilization.

Several studies conducted at the Subsurface Disposal Area (SDA) on the Idaho National Engineering Laboratory (INEL) suggest the importance of small mammals in this regard. Small mammals may encounter buried wastes or contaminated soil while burrowing (Arthur and Markham 1983, Arthur and Janke 1986). Also, vegetation on the SDA contains elevated levels of some radionuclides (Arthur 1982), which could be transferred to small mammals feeding on plant matter. These mechanisms have produced higher-than-normal radionuclide concentrations (Arthur et al. 1987) and dose rates (Arthur et al. 1986) for some SDA small mammals. Dispersal of these animals might result in export of radionuclides outside the waste site boundary (Groves and Keller 1983, Arthur et al. 1987). Small mammals are common prey items and could serve as vectors for transferring contamination to higher trophic levels. Arthur and Markham (1982) found elevated radionuclide concentrations in coyote scats collected near the site and suggested that ingested rodents were the source of contamination. Additionally, integrity of buried waste may be compromised when burrowing rodents deposit contamination on the soil surface (Arthur and Markham 1983, Boone 1990) where it is subject to wind and water erosion (Markham et al. 1978). Burrowing can also increase water infiltration into the soil profile (Day 1931, Laundré 1989, 1993) and thus into buried wastes.

Groves and Keller (1983) conducted the first detailed study of SDA small mammals in

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1978–79 and discovered that the site's highly modified habitat supported as great a density of small mammals as did surrounding native habitat. Their results also indicated that small mammals were more likely to be captured near the boundary than in the interior or in surrounding native sagebrush habitat (Groves 1981). Filipovich (1983) suggested a similar edge habitat preference by small mammals at another waste disposal site at the INEL. Further understanding of this phenomenon could provide information useful in reducing contact between rodents and buried wastes.

Our study was conducted at the SDA in 1988–89 with two objectives: (1) to examine temporal patterns of small mammal density and species composition on the site and compare these patterns to those in native habitat, and (2) to investigate spatial patterns of SDA small mammal distribution, particularly preferential utilization of edge habitat, and to assess movements across the site boundary between habitat types.

Study Area

The Idaho National Engineering Laboratory (INEL), established in 1949, is a U.S. Department of Energy reservation where numerous nuclear reactors and associated facilities are operated for research purposes. It is located in 230,000 ha of sagebrush desert on the Snake River Plain of southeastern Idaho. Temperature averages 5.6° C, with recorded extremes of 38° C and −44° C. Mean yearly precipitation is 22 cm, mostly snow or spring rain. Average elevation is approximately 1500 m.

The Radioactive Waste Management Complex (RWMC) is the major solid radioactive waste storage facility at the INEL. The SDA (36 ha) is that portion of the RWMC used for shallow land burial of radioactive waste. From 1952 to the present, solid wastes contaminated with fission and activation products have been interred at the SDA, with a minimum soil cover of 0.6 m (Markham 1978). Transuranic waste was also disposed of at the site until 1970. Various waste containers were utilized, including drums, bales, crates, and cardboard boxes.

The SDA is planted with nonnative crested wheatgrass (*Agropyron cristatum*, hereafter designated CWG). Russian thistle (*Salsola kali*) also is present in recently disturbed areas. The surrounding native vegetation type is big sagebrush (*Artemisia tridentata*)/ bluebunch wheatgrass (*Agropyron spicatum*) steppe (McBride et al. 1978).

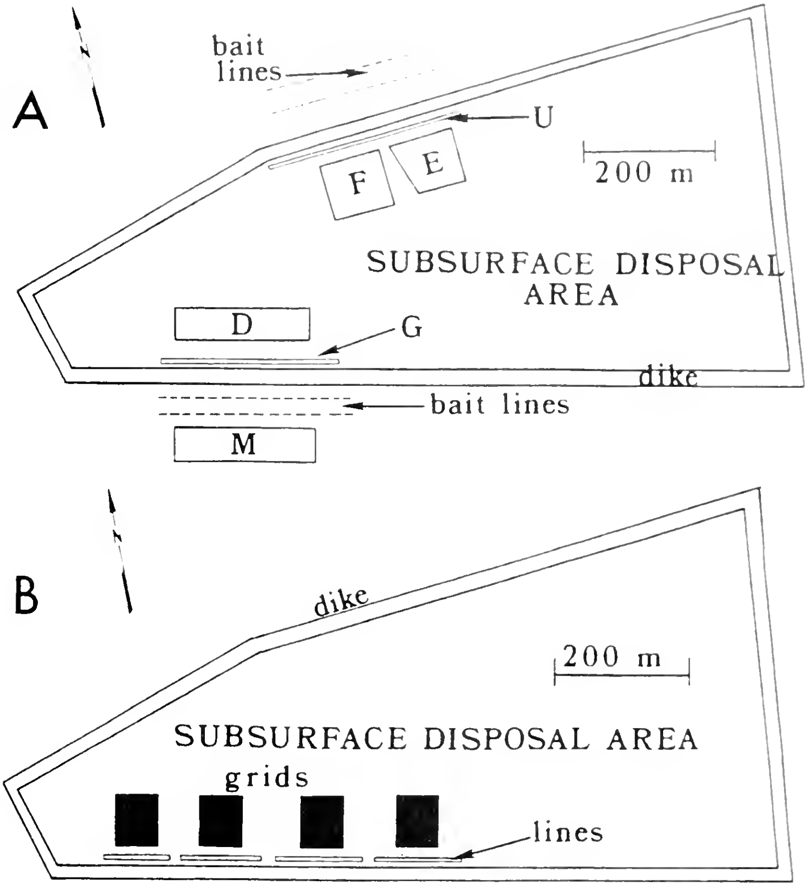
A perimeter earthen dike (constructed to reduce seasonal flooding) surrounds the area. Basalt boulders (up to 1.5-m diameter) reinforce its outer bank. CWG and Russian thistle, along with gravel and scattered lava rocks, are present on the dike's inner bank. The dike varies in height from 2 to 3 m, and distance from its inner to outer base is typically 25–30 m. Dirt roads are located on the top of the dike and along its inner and outer bases.

Methods

For the first field season (May–September 1988), live-trapping plots were chosen to duplicate as nearly as possible the location and configuration of trapping sites used by Groves and Keller (1983) in 1978–79. Three grids were established in CWG habitat in the SDA interior (Fig. 1A): grid D (100 stations, 5 × 20 configuration), grid E (105 stations, trapezoidal configuration), and grid F (100 stations, 10 × 10 configuration). Grid M (110 stations, 5 × 22 configuration) was located outside the SDA in native sagebrush habitat. Two lines of traps were placed along the inner base of the dike: line G (28 stations) on the south side and line U (30 stations) on the north. Distance between all stations was 10 m.

One Longworth live-trap was placed at each station. Nonabsorbent cotton nesting material was placed in each trap and changed frequently to reduce the possibility of trap aversion caused by odor of other rodents (Rowe 1970). Traps were baited with whole oats and covered with wooden boards to reduce temperature stress to captured animals. Prebaiting was performed prior to trapping sessions to familiarize animals with traps. Trapping sessions consisted of three consecutive nights of trapping. Newly captured rodents were marked on the ear with numbered fingerling tags. Each morning animals were recorded by trap location, species, tag number, sex, and weight, and then released at the point of capture.

Dyed-bait feeding stations (New 1958, Frantz 1972) were employed during the 1988 field season to investigate movements of small

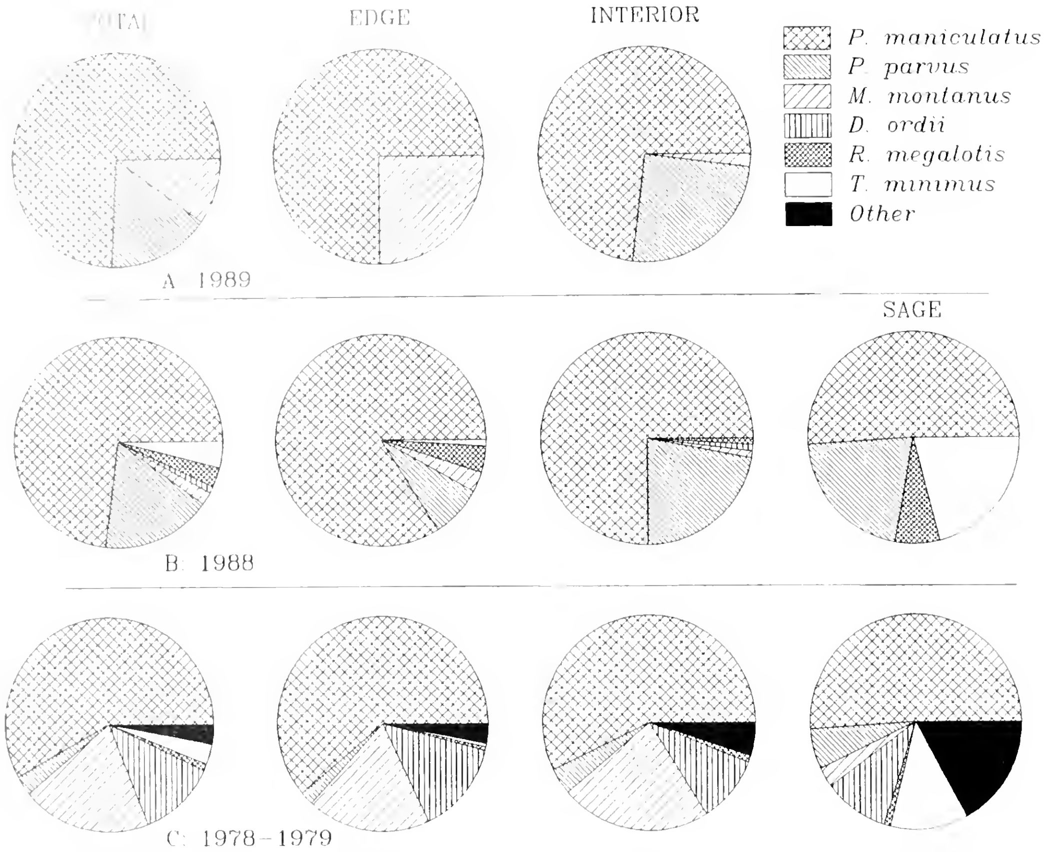


Figs. 1A–B. A: Location of trapping grids, trapping lines, and dyed bait feeding stations on the SDA in 1988. B: Location of trapping grids and lines in 1989.

mammals into and out of the SDA, using a modification of the Rhodamine B dye technique described by Evans and Griffith (1973). Paired lines of feeding stations were established outside SDA boundaries on the north and south sides (Fig. 1A), with stations situated at 5-m intervals. At each station an inverted plastic cup lid (9-cm-diameter) was secured to the ground by a nail to serve as a bait cup. Stations were baited with rolled oats sprayed with a 5% solution of Rhodamine B dye 3 days prior to a live-trapping session on the SDA. Rhodamine B, when ingested and handled by an animal, stains its pelage, feces, and urine red. Dye could be readily detected on animals if subsequently captured on the SDA.

In deference to the requirements of another facet of this study (Boone and Keller submitted), trapping configurations and procedures were altered somewhat for the second field season (June–September 1989). Four grids (16 stations each, 4 × 4 configuration) were located on the south portion of the SDA interior, and four dike lines (8 stations each) were established opposite the interior grids (Fig. 1B). No trapping in native sagebrush habitat was conducted.

All statistical tests followed Zar (1984). Tests of homogeneity of variances and normalcy fell within acceptable limits, allowing use of parametric procedures, except for diversity indices. Data were pooled over all sessions within each field season. Comparisons of densities between various areas were made with a measure of relative abundance (captures/100 trap nights) to reduce the effects of size and configuration differences between trapping



Figs. 2A–C. Species composition of small mammals at the SDA in edge habitat, interior crested wheatgrass habitat, adjacent sagebrush habitat, and across all habitats (total), based on percentage of individuals in 1989 (A), 1988 (B), and 1978–79 (C; from Groves and Keller 1983). Sage was not sampled in 1989.

grids and lines. The proximity of interior grids to edge lines (approximately 30 m) was intended to reduce excessive trapping "pressure" on edge lines attributable to the trapping edge effect (Tanaka 1980) by making both sampling sites potentially accessible to a given animal.

Results

In summer of 1988, 12 trapping sessions produced 521 captures of 144 individual small mammals. Six species were present (Fig. 2B). *Peromyscus maniculatus* was the most common small mammal, accounting for 72% of captures. *Tamias minimus* was common in sagebrush habitat but absent from the SDA. *Perognathus parvus* was the second most abundant rodent and was also common in sagebrush habitat. *Microtus montanus*, *Dipodomys ordii*, and *Reithrodontomys megalotis* were captured in small numbers. Mean captures/100 trap nights were significantly higher on SDA edge lines (36.2) than on CWG interior grids (17.6) for total small mammals ($p = .002$, two-sample t test) and for *P. maniculatus* (31.8 vs. 14.0, $p = .001$, two-sample t test).

Movement data in 1988 were collected only for *P. maniculatus*. Nearly half (41%) of the individuals captured on the SDA showed evidence of dye (Table 1), indicating that they had recently traveled outside the boundary. When possible, transients (animals captured on only one occasion) were eliminated from the calculation; 32% of the remaining *P. maniculatus* (assumed to be SDA residents) were known to have traveled outside the boundary.

In 1989, 20 trapping sessions produced 301 captures of 79 individual animals. Only

TABLE 1. Proportion of *P. maniculatus* captured within the SDA known to have traveled outside the boundary, 1988. Figures in parentheses are proportions after excluding possible transients. Figures in brackets are the numbers of animals.

Grid/Line	June	July	August
G	0.33 (0.33) [12]	0.40 (0.24) [25]	0.50 (0.50) [12]
D	0.38 (0.24) [29]	NA	0.52 (0.48) [21]
F	0.33 (0.11) [18]	NA	NA

Pooled $\bar{X}$ = 0.41 (0.32)
NA = data not available

three species were captured: *P. maniculatus*, *M. montanus*, and *Perognathus parvus* (Fig. 2A). *P. maniculatus* accounted for about 75% of captures on the SDA interior and edge. *M. montanus* was also captured on the edge and *P. parvus* in the interior. Captures/100 trap nights were significantly greater on edge lines (43.8) than on CWG interior grids (26.6) for total small mammals (p = .008, two-sample t test), and the difference was nearly significant for *P. maniculatus* (31.1 vs. 21.2, p = .07, two-sample t test).

Indices of small mammal density at the SDA and in adjacent native habitat were previously collected in 1978–79 (Groves and Keller 1983) and 1984 (Koehler and Anderson 1991). Biyearly density estimates for 1980–89 are also available for several native habitat sites around the INEL (B. L. Keller, unpublished data). SDA relative small mammal density (captures/100 trap nights) appeared to be similar in 1978–79, 1984, and 1988–89, although methodological differences between studies did not permit statistical comparisons (Fig. 3). Trap session estimates for total small mammals in 1988–89 ranged from 13.3 to 37.5 (mean = 23.9) on SDA interior habitat, and from 12.5 to 50.0 (mean = 40.9) on SDA edge. In 1984, 21.0 captures/100/trap nights (range 18.1–22.9) were reported on the interior (edge density was not calculated separately). For 1978–79, captures/100 trap nights had to be recalculated from pooled data (Groves 1981), so ranges could not be derived. Average density for the SDA interior was 27.0, and 47.3 for the edge.

Density of small mammals in native habitat immediately bordering the disposal site was similar to density on the interior in 1978–79, 1984, and 1988 (not sampled in 1989). In all three studies, however, sagebrush grids were located within 150 m of the boundary and therefore may have been influenced by SDA population trends. Keller's unpublished data for 1988 and 1989 indicate that relative densities of all rodent species in four sites across the INEL were typically about one-half the 1980–89 average levels (Fig. 4). In 1984, however, density on INEL plots was nearly average. Relative density in 1978–79 was estimated at average levels using the positive correlation of INEL rodent densities with precipitation totals for the preceding 12 months (R^2 = .61, p = .006). Rodents on and immediately around the SDA appeared not to have experienced the widespread decline in numbers that occurred across the INEL in 1988–89 (Fig. 4).

Although total density of SDA small mammals appeared to resist this widespread fluctuation, species composition varied somewhat between 1978–79 (Groves and Keller 1983) and 1988–89. These differences were a result of smaller densities of *M. montanus* and *D. ordii* in 1988–89 than in 1978–79 and a correspondingly greater proportion of *P. maniculatus* and *P. parvus* (Figs. 2A–C). In 1984 Koehler and Anderson (1991) also captured relatively few *M. montanus* on the SDA, though *D. ordii* numbers were similar to 1978–79 levels. On a smaller INEL waste site in 1981–82, Filipovich (1983) noted a species composition intermediate to 1978–79 and 1988–89 SDA results. Keller (unpublished data covering 1980–89) documented lower-than-average numbers of *M. montanus* and *D. ordii* on the INEL in 1988–89. Eight species were trapped on the SDA in 1978–79, while only five occurred in 1988–89. Shannon-Weaver diversity indices in 1988–89 averaged 0.62 for interior grids and 0.53 for edge lines, while in 1978–79, average values for the interior and edge were 1.01 and 1.22 (significant difference at p = .046 for interior, p = .002 for edge; Mann-Whitney test).

DISCUSSION

Integration of the data from this study with previously collected information suggests that small mammal density at the SDA was "buffered" somewhat against surrounding

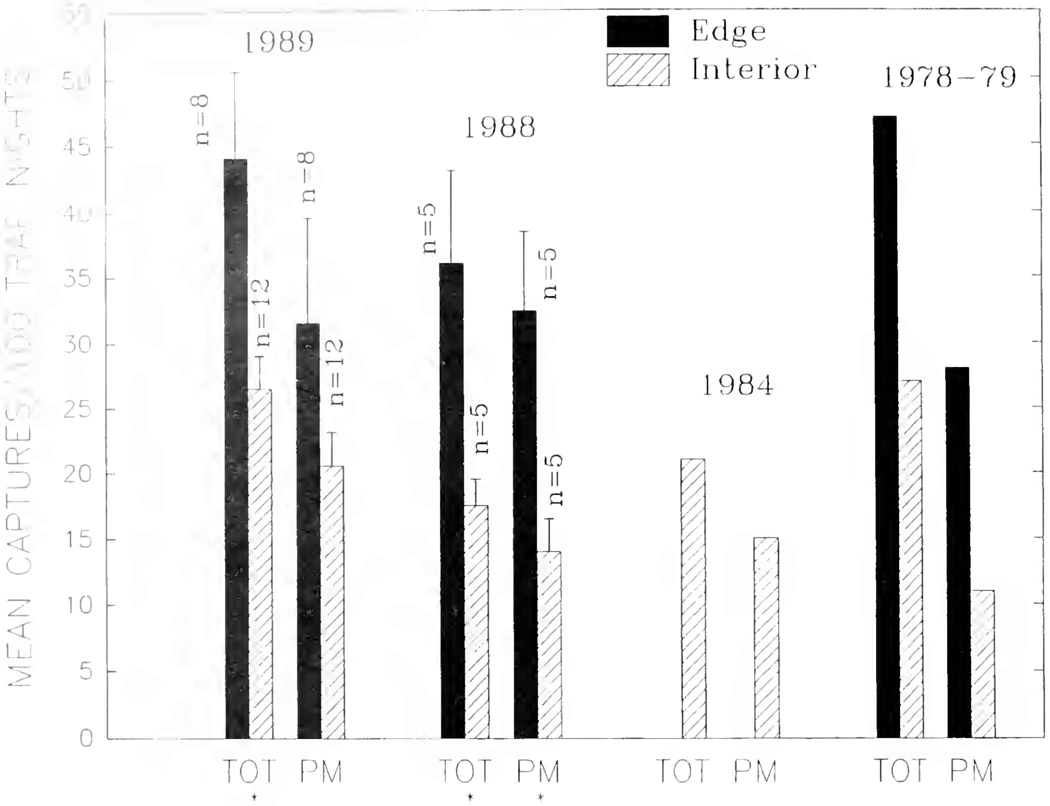


Fig. 3. Mean captures/100 trap nights for all small mammals (TOT) and *P. maniculatus* on SDA edge and interior grids for 1989, 1988, 1984 (from Koehler and Anderson 1991) and 1978–79 (from Groves 1981). Error bars are 1 SE, *n* values are number of trapping sessions, and asterisks represent significant differences ($p < .05$, *t* test) between edge and interior grids. Standard errors and significance values could not be calculated for 1984 and 1978–79 because only mean values were available and edge habitat was not trapped in 1984.

temporal fluctuations. As numbers of all species declined over the INEL, *P. maniculatus* and *P. parvus* on the SDA were able to maintain (and possibly slightly increase) their densities, resulting in a relatively constant overall small mammal density. It appears that some SDA feature(s) allowed these species to avoid widespread population declines and perhaps benefit from reduced numbers of potential competitors.

Beatley (1969) states that precipitation can cause fluctuation of rodent densities in desert ecosystems indirectly through its impact on vegetation. Adverse impacts of drought are most severe for species with narrow habitat preferences, while species with greater tolerances (such as *P. maniculatus*) often increase in density (Whitford 1976). This suggests a model consistent with events on the INEL in 1988–89. The presence of two distinct habitat types near the SDA may have provided a diverse foraging base affected less severely by drought than food supplies in comparatively uniform sagebrush habitat. Animals residing near the habitat edge would have access to CWG seeds when abundant, yet be able to utilize native habitat during other periods. SDA populations of *P. maniculatus* and *P. parvus* may have been primary beneficiaries of such a phenomenon because both species are relative generalists that utilize both sagebrush and CWG habitats, whereas other species (*M. montanus, D. ordii, T. minimus*) tend to have more specific habitat preferences. *P. maniculatus* have, in fact, been observed to utilize CWG seeds heavily during periods of abundance on the INEL (Filipovich 1983, Koehler and Anderson 1991).

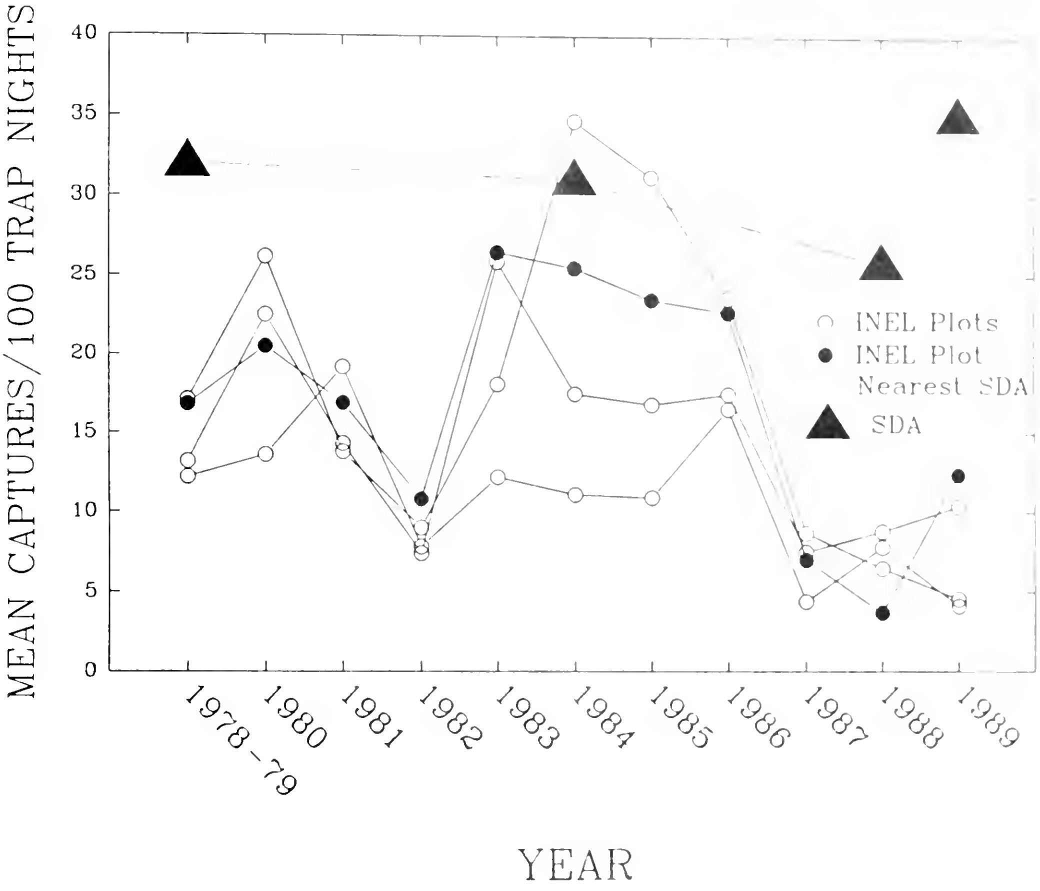


Fig. 4. Trends in density of all INEL small mammals (from B. L. Keller unpublished data) compared [illegible] density at the SDA. INEL data for 1978–79 are estimates (see text). Lines between SDA data points [illegible] and do not represent observed density trajectories. SDA data are weighted averages of edge and interior habitat [illegible] 1978–79 and 1988–89. The 1984 data point (based on interior sites only) was weighted by the average [illegible] ratio from 1978–79 and 1988–89.

This model could explain the elevated density of *P. maniculatus* in SDA edge habitat (it was difficult to determine how well *P. parvus* fit the model because of relatively low numbers). Although use of trapping lines at the boundary may have amplified the observed differences with interior trapping grids, the magnitude of such methodological artifacts is typically much lower than the twofold ratio we recorded (Tanaka 1980). Furthermore, no trapping "edge effect" was observed for exterior versus interior trapping stations on SDA trapping grids during our study, although there was a tendency for traps nearest the boundary to be most successful.

Unimpeded movements by small mammals between habitat types are required to hypothesize an edge preference based on diversity of food sources. It has been suggested that open roadways are an impediment to rodent movements (Oxley et al. 1974), though the roads implicated in this effect were somewhat wider than the road on top of the SDA dike. Earlier investigations documented frequent small mammal movements on the order of 100 m into and out of the SDA (Groves and Keller 1986, Koehler 1988). Results of our study indicate that enlargement of the perimeter dike in the 1980s did not substantially reduce small mammal movements across the boundary. Frequency of movements by *P. maniculatus* across the dike suggests that both habitat types are visited, and presumably utilized, by this species. The method we employed did not allow determination of relative foraging efforts expended on each habitat type by individual animals, or the scale and duration of movements. The model discussed above would predict that allocation of foraging effort should vary seasonally as well as yearly.

Thus, the presence of edge habitat appears to be an important factor encouraging utilization of the SDA by certain small mammal species and buffering overall density fluctuations. This edge preference potentially could be used to reduce both utilization of SDA habitat by rodents and ensuing contact with radioactive waste. It is not practical to reestablish native habitat on the SDA because of frequent surface disturbances. Additionally, CWG is desirable at waste sites because it provides rapid anchoring of fill dirt and effectively removes water from lower soil levels. A more promising alternative is extending CWG plantings outside the boundary. With edge habitat sufficiently removed from the SDA, highest rodent densities would be expected away from buried wastes. Increasing the size of CWG habitat might, however, result in a greater density of *M. microtus*, which prefers CWG at the INEL and exhibits regular population cycles and the associated peak densities in some areas. No cycles have been confirmed for this species at the INEL, but this may be because available patches of CWG are too small to support a cycling population. Peak populations of this species at the SDA could pose additional problems for waste managers. An indirect test of the utility of extending CWG planting at the disposal site is discussed elsewhere (Boone and Keller submitted).

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PHYTOPLANKTON IN A HIGH-ELEVATION LAKE, COLORADO FRONT RANGE: APPLICATION TO LAKE ACIDIFICATION

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ABSTRACT.— The purpose of this research was to evaluate the status of phytoplankton in Lake Albion in the Green Lakes valley, Colorado Front Range, with respect to lake acidification. The research was conducted during the inventory phase of the Long-Term Ecological Research program of the University of Colorado at the Niwot Ridge/Green Lakes valley site. Lake Albion is a small subalpine lake on the terminal end of the Green Lakes valley (13 ha, mean depth 6 m, and surface pH 6.51). Net plankton were collected six times during June–August 1984. Ancillary data on nutrients, temperature, chlorophyll *a*, and Secchi disc transparency were also obtained. Diatoms were identified and assigned to categories based upon their known tolerances to hydrogen ion concentration. The diatom flora was composed mostly of alkaliphilic or species indifferent to hydrogen ion concentration, a characteristic Lake Albion shares with other Front Range lakes. The diatom flora and water chemistry of Lake Albion are compared to other high-elevation lakes.

Key words: phytoplankton, diatoms, lake acidification, nutrients, subalpine lake, flagellates, Colorado.

Although alpine lakes have been studied intensively in Europe (Pechlaner et al. 1972, Bretschko 1975, Martinez-Silvestre 1975, Rott 1988), little recent limnological information is available for North America. This is particularly regrettable since alpine lakes in western North America may be influenced by acid deposition (Lewis 1982, Kling and Grant 1984, Stauffer 1990). Thus, there is a need to study these lakes before their water chemistry is altered.

Research to be described had original objectives within the Long-Term Ecological Research (LTER) program of the National Science Foundation. The University of Colorado, Niwot Ridge/Green Lakes valley LTER site is the only alpine site in the national network. This paper reports species composition of phytoplankton for the terminal mountain lake in this catchment, collected during the program's inventory phase. The objective was to determine species composition of phytoplankton, particularly diatoms, for the purpose of identifying relative acid tolerance of the assemblage.

Freshwater diatoms are good indicator organisms of water quality including pH (Lowe 1974). Their distribution in present and past aquatic habitats has been a valuable tool to identify historical changes in water chemistry and thus infer possible changes in climate and/or land use. Diatoms are now used to infer changes in water chemistry due to lake acidification. Predictive equations or indices have been developed that relate diatom assemblages to pH (Nygaard 1956, Renberg and Hellberg 1982, Charles 1985, Baron et al. 1986). While it is not possible to determine how pH or related factors control diatom assemblages, the predictive ability of these indices is very strong (Charles 1985).

A second objective was to describe the physical/chemical limnology of the lake. While stream water chemistry has been well studied in the Green Lakes valley, little information is available for the lakes.

STUDY AREA

Lake Albion is located at 3299 m in the Green Lakes valley, Colorado Front Range, 40°2'49"N, 105°36'11"W (Monarch Lake Quadrangle). The watershed (7.1 km^2) is divided into two basins by a steep bedrock step between Green Lakes 3 and 4 (Fig. 1). The upper valley (2.0 km^2) has steep-sided rock walls, talus slopes, and a valley floor on glaciated bedrock. The lower valley (5.0 km^2) is the catchment basin between Green Lake 4 and Lake Albion. Here the valley sides have more gentle slopes and greater soil depth than the upper valley. In the lower valley trees are

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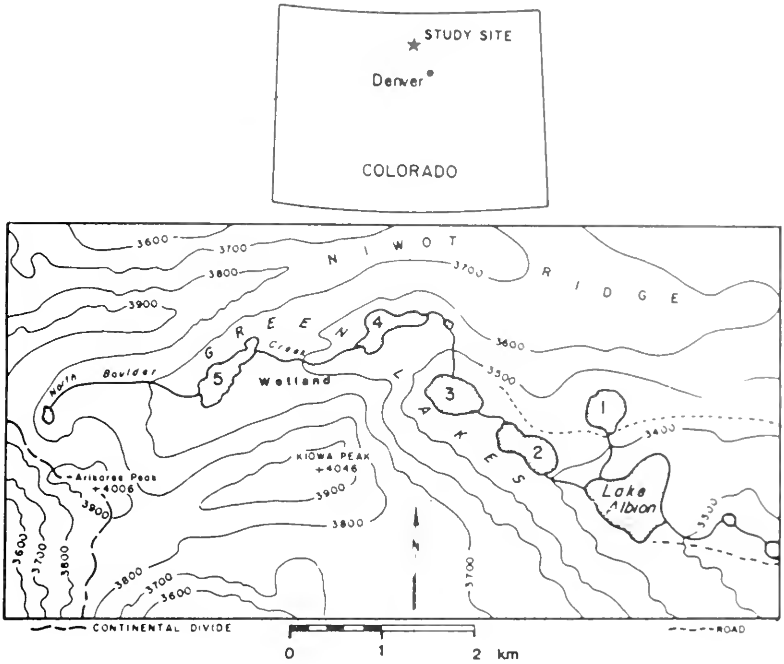

Fig. 1. Location map of study area in the Green Lakes valley, Colorado Front Range.

present, but most are dwarfed or flagged. Lake Albion has an area of 13 ha, a mean depth of 6.0 m, and a maximum depth of 14 m.

METHODS

One permanent sampling station was established in Lake Albion where the depth was 14 m. Except for nutrients, the lake was sampled six times between 21 June and 9 August 1984. Nutrient samples were taken on 28 June, 5 and 12 July. Diatoms frequently flourish in Colorado mountain lakes during this period (Olive 1953, McKnight et al. 1990). Net phytoplankton was sampled by taking two vertical tows of the water column with a conical plankton 10-μm mesh net. Phytoplankton nets are selective for only large plankters (Wetzel and Likens 1979) but were used in this research to obtain samples of the entire water column. Algae are frequently stratified in mountain lakes, particularly motile flagellates, and might be missed with bottle samplers (Rott 1988). Samples were preserved in Lugol's solution.

Water temperature was measured at meter intervals with a thermistor telethermometer, and Secchi disc depth was obtained with a 10-cm black white disc. Samples for chlorophyll *a* and nutrients were obtained with a PVC Kemmerer bottle at the surface, at 3, 6, and 9 m, and near the bottom (13.5 m) and stored in polypropylene bottles. Grab samples for nutrients were also taken at the inlet and outlet.

Each algal sample was examined microscopically for 1 h to obtain a species list. Diatom frustules were cleared with HNO_3 and $K_2Cr_2O_7$, and permanent mounts with Hydrax were made for microscope examination. Taxa were assigned to pH groups normally used (Charles 1985) following Hustedt (1939):

Acidobiontic—optimum distribution at pH below 5.5; occur only in acidic habitats
Acidophilic—widest distribution at pH less than 7
Indifferent (circumneutral)—distributed around pH 7
Alkaliphilic—widest distribution at pH greater than 7
Alkalibiontic—occur only at pH greater than 7

[illegible] pH and presence in samples during 1984. Sensitivity*
+ = present

		Present in the sample					
	Sensitivity*	21 Jun	28 Jun	5 Jul	12 Jul	23 Jul	9 Aug
[illegible]	ALKF IND	+	+		+		
[illegible]	ALKF IND		+	+	+		
[illegible]	ACF					+	
[illegible]			+	+			
[illegible]		+	+		+		
[illegible]	ALKF	+	+		+		
[illegible]	ALKF IND		+				
[illegible]	ALKF	+	+	+	+	+	+
[illegible]		+					
[illegible]		+					
[illegible]		+	+		+		
[illegible]		+	+	+	+	+	
[illegible]	ALKF				+		
[illegible]		+	+				
[illegible]			+				
[illegible]	ALKF			+			
[illegible]	ALKF		+				
[illegible]	ALKF		+	+			
[illegible]	ALKF IND	+	+	+	+		
[illegible]	ALKF IND	+	+	+	+	+	+
[illegible]		+					
[illegible]	ALKF			+			
[illegible]	IND			+			
[illegible]	ALKF		+			+	+
[illegible]	IND	+		+	+	+	
[illegible]	IND				+		
[illegible]	IND	+	+		+		+
[illegible]	ALKF IND				+		
[illegible]			+				
[illegible]	ALKF	+	+	+	+	+	+
[illegible]	ALKF,ALKB	+	+	+	+	+	+
[illegible]							+
[illegible]	ALKF IND	+					
[illegible]	ACF		+	+	+		+
[illegible]				+	+		
[illegible]	ACF	+	+	+	+	+	
[illegible]	ACF				+		
[illegible]	ACF	+			+		
[illegible]		+					+
[illegible]	ALKF				+		
[illegible]	ALKF IND			+			
[illegible]		+					
[illegible]	ALKF	+		+			
[illegible]	ACF	+	+	+	+		+
[illegible]	ACF		+				
[illegible]	ALKF IND					+	+
[illegible]	ALKF IND	+					
[illegible]	ALKF IND					+	
[illegible]					+		
[illegible]					+		
[illegible]	IND					+	
[illegible]	IND		+		+		
[illegible]	ALKF IND	+	+	+	+	+	+
[illegible]	ALKF	+	+		+		

TABLE 1. Continued.

Taxon	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
Navicula gracilloides A. Mayer			+				
laevissima Kutz.	IND				+		
minima Grun.	IND, ALKF		+	+			
notha Wallace	ACF	+	+	+			+
pseudoscutiformis Hust.	IND		+		+		+
pupula var. *mutata* (Krasske) Hust.					+	+	+
pupula var. *rectangularis*	IND	+					
radiosa Kutz.	IND	+		+	+	+	+
seminulum Grun.	IND	+					
Navicula sp.			+	+	+		+
Neidium iridis var. *ampliatum* (Ehr.) Cl.	IND				+		
Neidium sp.			+	+			
Nitzschia acuta Hantzsch	ALKF, IND			+	+		+
amphibia						+	
fonticola Grun.	IND			+			
palea (Kutz.) W. Sm.	IND	+	+		+	+	+
thermalis var. *minor*				+			
Nitzschia sp.		+	+	+	+		
Pinnularia borealis Ehr.	IND	+		+			
legumen Ehr.			+				
major (Kutz.) Rabh.			+				
mesolepta (Ehr.) W. Sm.							+
mesolepta var. *angusta* Cl.		+					
microstauron var. *ambigua* Meister			+	+			
microstauron (Ehr.) Cl.	ACB, ACF				+		
subcapitata Greg.		+	+	+	+	+	+
Pinnularia sp.				+	+	+	+
Rhizosolenia eriensis H. L. Smith	ALKF	+	+	+	+		
eriensis var. *morsa* W. et G. S. West				+			
eriensis var. *tenuis* Hust.		+	+	+			
nana Kiss				+			
Stauroneis anceps f. *gracilis* Rabh.	ACF, IND	+		+	+		
phoenicenteron f. *gracilis* (Ehr.) Hust.	IND		+				
phoenicenteron (Nitz.) Ehr.	IND		+	+	+		
smithii Grun.	ALKF, IND				+		
Stephanodiscus sp.		+	+	+	+		
Surirella biseriata var. *bifrons* (Ehr.) Hust.			+				
Surirella sp.		+	+		+		
Synedra filiformis var. *exilis* Cl.-Eul.	ALKF						+
incisa Boyer		+	+	+	+	+	+
rumpens Kutz.	IND	+	+				
ulna (Nitz.) Ehr.	ALKF	+	+	+		+	+
Synedra sp.		+	+	+	+		
Tabellaria fenestrata (Lyngb.) Kutz.	IND, ACF	+	+	+	+	+	+
flocculosa (Roth) Kutz.	ACF	+	+	+	+	+	+
Tetracyclus lacustris Ralfs				+			

*[illegible] = [illegible]
ALKF = [illegible] ALKB = [illegible]

Literature references were used to assign taxa to these categories (Hustedt 1939, Nygaard 1956, Patrick and Reimer 1966, Lowe 1974, Charles 1985). Slides were deposited in the Diatom Collection of the California Academy of Science. Relevant slide numbers are 216082–216087.

Water for nutrient analyses was filtered through prerinsed Reeve Angel glass [illegible]

[illegible]

TABLE 2. Flagellated taxa observed in Lake Albion during 1984 by date.

CHRYSOPHYCEAE	
Bitrichia longispina Lund Bourr.	6/21, 6/28, 7/5, 7/12, 7/23, 8/9
Dinobryon sertularia Ehr.	6/21, 6/28, 7/5, 7/12, 7/23, 8/9
Dinobryon suecicum var. *longispinum* Lemm.	6/21, 6/28, 7/5, 7/12
Mallomonas sp. 1	All dates
Mallomonas sp. 2	6/21, 6/28, 7/5, 7/12, 7/23, 8/9
Mallomonas sp. 3	6/28
Uroglena cysts?	6/21, 6/28, 7/5, 7/12, 7/23
DINOPHYCEAE	
Gymnodinium sp.	6/28
Peridinium lomnickii Wol.	6/28
Peridinium umbonatum Stein	7/5, 7/12, 7/23, 8/9
Peridinium volzii Lemm.	6/21, 6/28, 7/5
CRYPTOPHYCEAE	
Cryptomonas sp. 1	All dates
Cryptomonas sp. 2	6/21, 6/28, 7/12, 7/23, 8/9

sulfanilamide method, and ammonia colorimetrically using a phenol-hypochlorite method.

Known volumes of lake water were filtered onto precombusted (525°C, 2 h) RAGF for analyses of chlorophyll *a* (chl. *a*). Chlorophyll *a* samples were stored in paper envelopes in the dark at –5°C until 15 October, when analysis was completed using the monochromatic method to convert absorbance in a 1-cm cell to chl. *a* concentrations (Wetzel and Likens 1979). Values reported here were corrected for phaeopigments.

RESULTS

Presence-absence data for net phytoplankton revealed that numbers of both diatom species and genera were high, with pennate diatoms being more important than centric diatoms (Table 1). Although no attempt was made to determine density, the most frequently encountered taxa in Lake Albion were *Rhizosolenia* spp., *Asterionella formosa* Hass., and *Cyclotella* spp. Eighty-five taxa were identified to species.

Sensitivity to pH was determined for 73% of the species identified (Table 1). About 59% of Lake Albion species were indifferent, indifferent to acidophilic, or indifferent to alkaliphilic. About 22% were alkaliphilic and 8% were acidiphilic. One species of *Diatoma* was classified by Lowe (1974) as alkaliphilic to alkalibiontic, and one species of *Pinnularia* was classified as acidiphilic to acidibiontic. The pH tolerance of 27% of the species remains unknown.

Caine and Thurman (1990) report that during 1982–87 the mean pH of surface water of Lake Albion was 6.51 (standard deviation 0.28, n = 151). Thus, the 1984 diatom assemblage reflects the slightly acidic conditions of the lake, although fully 22% of the taxa were reported to have their widest distribution at pH values above 7.

While diatoms are good indicators of pH, chrysophytes are also sensitive to acidification (Charles and Smol 1988). There is a report of a flagellate, *Gonyostomum semen*, increasing to nuisance densities in Swedish forest lakes (Cronberg et al. 1988). Thus, Table 2 lists flagellated taxa for future reference.

The Secchi disc depth in Lake Albion ranged from 2.2 m on 12 July to 2.8 m on 21 June ($\bar{x}$ = 2.55 m, 95% confidence interval 2.39–2.71 m). Water temperature was isothermal with respect to depth. The mean temperature of the water column advanced with the growing season from 5.9°C on 21 June to 10.3°C on 9 August.

Chlorophyll *a* concentrations rose during July and reached a maximum on 23 July (Table 3). Chlorophyll *a* concentrations were isochemical with respect to depth, except on 23 July, when concentrations below 6 m were about twice as high as those at 0.5 and 3 m.

The concentration of SRP on 28 June was 180 μg L^{-1} at 3 m, while the concentration at other depths was less than 25 μg L^{-1} (Table 4). On 5 July SRP concentrations were also higher at 3 and 6 m (189 and 190 μg L^{-1}) than at other depths where concentrations were less than 30 μg L^{-1}. All other nutrients were isochemical with respect to depth (Table 4).

DISCUSSION

The results of this study are similar to another study of fossil diatoms in lakes in Rocky Mountain National Park where the diatom flora was alkaliphilic or indifferent in four lakes (Baron et al. 1986). Baron et al. (1986) were able to reconstruct the pH history of the lakes using sedimentary cores and concluded there was no historical evidence of pH changes

TABLE 3. Concentration of chlorophyll *a* as micrograms L⁻¹ in Lake Albion during 1984. ND = no data.

Depth (m)	21 June	28 June	7 July	12 July	[illegible] July	[illegible] Aug
0.5	2.6	3.2	4.4	2.9	[illegible]	[illegible]
3	2.7	3.1	3.6	3.4	[illegible]	[illegible]
6	2.8	3.4	3.4	4.5	[illegible]	[illegible]
9	2.6	3.4	ND	2.9	7.0	[illegible]
13.5	2.8	4.5	ND	4.7	6.4	[illegible]

TABLE 4. Concentration of nutrients in Lake Albion during 1984 as micrograms N or P L⁻¹. SRP = soluble reactive -P; NH_4+ = ammonia -N + ammonium -N. ND = no data. U = undetected.

Depth	28 June				5 July				12 July			
(meter)	SRP	NO_3^-	NO_2^-	NH_4^+	SRP	NO_3^-	NO_2^-	NH_4^+	SRP	NO_3^-	NO_2^-	NH_4^+
0.5	19	38	6	33	20	16	[illegible]	35	ND	ND	ND	ND
3.0	180	34	3	29	189	55	[illegible]	30	ND	ND	ND	ND
6.0	24	40	2	21	198	65	1	36	36	50	5	[illegible]
9.0	19	42	2	33	30	76	5	37	45	50	1	[illegible]
13.5	19	40	3	13	20	65	5	35	49	1	[illegible]	15
Inlet	20	874	2	17	18	124	5	37	50	90	5	[illegible]
Outlet	18	21	3	23	20	33	1	32	49	40	1	[illegible]

due to acid deposition. The pH history of Lake Albion may be similar.

One limitation of the Lake Albion data stems from the procedure of assigning diatoms to pH categories using literature sources. Charles (1985) found that the predictive strength of multiple regression equations was greater when assignments of diatoms to pH categories were based upon known values of pH in lake waters where collections were made rather than upon literature values.

The presence/absence data for Lake Albion diatoms are compared below to other high-elevation lakes at similar latitudes in North America where extensive data sets are available. Bateman and Rushforth (1984) studied the periphytic diatom flora of 53 lakes in the Uinta Mountains of Utah. Collections were made during July–September 1982. Lakes were located between 2316 m and 3353 m. McKnight et al. (1986) studied the phytoplankton of Sky Pond and The Loch in Rocky Mountain National Park, Colorado. Both lakes are in the Loch Vale watershed, which has been intensively studied with respect to acid deposition. Phytoplankton were collected in 2–3 tows of a 40-mesh size net at 14-day intervals between 5 June and 30 August 1984. Sky Pond is located at 3322 m, surface area 3.03 ha, while The Loch is located at 3048 m, surface area 4.98 ha.

Fourteen diatom species were observed in Lake Albion five or more times (Table 5). Eleven of these same species were also observed in Uinta Mountain lakes and 8 in Sky Pond and/or The Loch. Bateman and Rushforth (1984) assigned importance values to diatoms collected from Uinta Mountain lakes and list 14 of the most common species. Only 50% of these species were also observed in Lake Albion. Those not observed were *Achnanthes austriaca*, *Anomoeoneis serians* var. *brachysira*, *Fragilaria construens* var. *venter*, *Frustula rhomboides* var. *undulata*, *Nitzschia minutula*, *Nitzschia paleacea*, and *Pinnularia brebissonii* var. *diminuta*.

The total number of species observed in Uinta Mountain lakes was 241, of which 45 or 19% were observed in Lake Albion. The total number of species observed in Sky Pond and The Loch was 13 and 53, respectively. The percentage of species in Sky Pond and The Loch in common with Lake Albion was [illegible] and 11%, respectively. Bateman and Rushforth (1984) found a low index of similarity (17%) between lakes in the Utah study.

The diatom flora of the Uinta Mountain lakes may have been less similar to Lake Albion because some bog lakes were included in the Utah study and also because periphyton, not phytoplankton, was examined in the Utah study. *Asterionella formosa* Hass. was

TABLE 5. Diatom species observed in samples from Lake Albion five or more times and their presence (+) in other high-elevation lakes.

	Utah	Colorado	
Lake Albion	Uinta Mountains	Sky Pond	The Loch
Asterionella formosa Hass.	+	+	+
Aulacoseira italica (Ehr.) Simonson			
Cyclotella stelligera Cl. & Grun	+	+	+
Diatoma anceps (Ehr.) Kirch.	+	+	+
Diatoma hiemale var. *mesodon* (Ehr.) Grun.	+		+
Eunotia perpusilla Grun.			
Frustulia rhomboides (Ehr.) DeT.	+	+	+
Hannaea arcus (Ehr.) Patr.	+		+
Navicula radiosa Kütz.	+		+
Nitzschia palea (Kütz.) Wm. Sm.	+		
Pinnularia subcapita Greg.	+		
Synedra incisa Boyer			
Synedra ulna (Nitz.) Ehr.			
Tabellaria flocculosa (Roth.) Kütz.	+		+

the most common diatom in Sky Pond, The Loch, and Lake Albion but was rarely encountered in the Uinta Mountain lakes. This result reflects the difference between benthic and pelagic habitats sampled.

Euplanktonic diatoms were limited to Adirondack lakes with pH in excess of 5.8 to 6.0, but benthic diatoms existed in lakes at pH <6.0 (Charles 1985). Sampling sediments for diatoms to infer pH changes in lakes has the advantage of integrating species from both habitats, but the disadvantage that diatoms in surface sediments from mid-lake samples may not be in proportion to diatom density in those habitats (Meriläinen 1971). Further research in alpine paternoster lakes is needed to determine the relative contribution of lotic benthic diatoms to lake assemblages to identify true euplanktonic assemblages.

The high SRP values in Lake Albion are likely to be correct because they occurred on two dates at the same depth range (McKnight personal communication). The same phenomenon was also observed in The Loch and Sky Pond by McKnight et al. (1986). The reason for the high values is unknown.

Chlorophyll *a* concentrations observed in Lake Albion were not corrected for storage and are underestimates since chlorophyll *a* estimates may decrease by 40% in 56 days due to storage (Toetz unpublished data). Even so, the range of values for Lake Albion in July is similar to the range of values for The Loch and Sky Pond during the same year (McKnight et al. 1986).

It is not possible to make more meaningful comparisons between Lake Albion and other high-elevation lakes because sampling procedures were not standardized. However, all indications are that Lake Albion, Sky Pond, and The Loch are not grossly dissimilar. Thus, any large-scale environmental change may produce somewhat similar effects in all three.

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EFFECTS OF SOIL STRUCTURE ON BURROW CHARACTERISTICS OF FIVE SMALL MAMMAL SPECIES

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ABSTRACT.— Burrows of small mammals can impact a variety of soil processes including organic turnover, aeration, and mineralization rates. The structure of burrows, depth, length, and complexity can influence the extent of the impact burrows have on soil processes. Soil properties, in turn, are thought to affect burrow structure. To increase our understanding of burrow-soil dynamics, we compared maximum depth, total volume, total length, volume:length ratio, and complexity of burrows of five small mammal species with bulk density and soil texture in multiple regression analyses. Burrows of Wyoming ground squirrels (*Spermophilus elegans*) were deeper, longer, and more complex as percentage of silt and clay increased and percentage of sand and bulk density decreased. Average maximum depth of montane vole (*Microtus montanus*) burrows increased as soils became sandier. Length and volume of deer mice (*Peromyscus maniculatus*) burrows increased with increases in bulk density and percentage of clay. Volume, length, and complexity of kangaroo rat (*Dipodomys ordii*) burrows were greater in soils with higher amounts of clay and silt. Townsend's ground squirrel (*Spermophilus townsendii*) burrows did not appear to be affected by the soil properties measured.

Key words: burrow structure, soil, small mammals, bulk density, soil texture, Idaho.

The association between burrowing activity of mammals and the subterranean environment is an interdependent relationship that is receiving increasing attention because of its potential impact on plant community structure (Andersen and MacMahon 1985, Inouye et al. 1987). Burrowing activity of mammals can impact a variety of soil processes including organic matter turnover, inorganic distribution, aeration, and mineralization rates (Abaturov 1972, Chew 1978, Zlotin and Khodashova 1980, Hole 1981, Reichman and Smith 1989). The extent to which burrowing mammals may influence soil processes can depend on the structure (complexity and dimensions) of burrow systems. Deeper burrows increase the depth, and more extensive, convoluted burrows increase the area of influence compared with shallower and simpler systems. Thus, factors that influence burrow structure could ultimately determine the impact a burrow has on soil processes in an area.

Burrow structure varies considerably among species (Reynolds and Wakkinen 1987, Reichman and Smith 1989) and also differs within a species with length of occupation of the burrow or age of occupant (Reichman and Smith 1989). Intraspecific differences in burrow dimensions are also hypothesized to be related to physical properties of soils, e.g., bulk density, texture, etc. (Anderson and Allred 1964, Reynolds and Wakkinen 1987). However, this hypothesis has not been adequately tested. To more clearly understand the dynamic relationship between burrowing mammals and the soil they live in, more information is needed on how soil characteristics impact burrow structure. Assuming soil properties impact burrow structure, we predicted that burrow dimensions within a species should be quantitatively related to changes in measurable soil attributes. The purpose of this research was to test this prediction.

STUDY AREA AND METHODS

To test our prediction, data of Reynolds and Wakkinen (1987) were supplemented with data on burrows from several other soil types. All data came from within two study areas in southeastern Idaho: the Idaho National Engineering Laboratory (INEL), 65 km NNW of Pocatello, Bannock County, and public and private lands near Soda Springs, Caribou County. The INEL, a National Environmental Research Park on the upper Snake River plain, is classified as a cool sagebrush

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(*Artemisia* spp.) desert dominated by sagebrush and grasses (Anderson and Holte 1981). Sample sites near Soda Springs were in three mountain valleys: Wooley Valley, T33N, R43E, Sec. 25; Conda Valley, T8S, R42E, Sec. 23; and Big Canyon, T9S, R43E, Sec. 13. Vegetation at these sites is also a sagebrush-grass mixture.

Multiple regression analysis was used to test the prediction that burrow dimensions within a species are quantitatively related to changes in soil properties. Measurements of each burrow characteristic taken were individually used as the dependent variables; properties of the soils found at corresponding burrow sites were the independent variables. The null hypothesis tested for each analysis was that the multiple regression coefficient was equal to zero.

For each species, burrows were excavated from at least four different subsites, representing a variety of soil types, within the study areas. Subsites were selected based on the presence of burrows in the area. Within the subsites, usually all the burrows were sampled. To quantify soil differences among burrow sites within a species, we measured bulk density (g/cm^3) and soil texture (percent sand, silt, and clay) at approximately 10 cm below the soil surface at burrow locations with the core technique (Blake 1965) and the hydrometer technique (Day 1965), respectively. Soils in the study areas had relatively uniform profiles with little vertical development, so near-surface measurements were considered adequate to classify the soil profile. It is recognized that other soil properties exist and might influence burrowing behavior. However, estimates of density and texture are easily obtained, and other properties such as drainage, structure, and consistency are correlated with these two measurements (Foth 1978).

The measurements we took to quantify the soils are highly correlated and would not be appropriate for use in a regression analysis. To classify soil types based on uncorrelated indices, we used the data on bulk density and soil texture to generate z-score standardized principal component scores (Manly 1990) for each soil sample taken at burrow sites. We then used the first two principal components (soil components) as the uncorrelated independent variables in our regression analyses. All principal component analyses (PCA) were conducted with the Biostat I (Sigma Soft, 1430 Shadowood Land, Placentia, CA 92670) statistical package.

Burrows of five small mammal species were included in this study: Townsend's ground squirrel (*Spermophilus townsendii*), Wyoming ground squirrel (*S. elegans*), deer mouse (*Peromyscus maniculatus*), Ord's kangaroo rat (*Dipodomys ordii*), and montane vole (*Microtus montanus*). Before we examined a burrow system, we determined the species occupying the burrow by making visual observations, snap-trapping, or examining hair and feces near burrow entrances. Little data were available on the age of burrow occupants. Of the animals taken with snap-traps, most were adults. We injected the burrows with polyurethane foam (Felthauser and McInroy 1983), excavated the surrounding soil, and measured the burrow system.

Five measurements were recorded: maximum depth, total length, volume, volume:length ratio, and complexity. Maximum burrow depth to the bottom of the burrow was determined by measuring depth in situ at 10-cm intervals along the total length of the exposed foam casts. Total burrow length was the sum of the main and all side tunnels. After depth and length were recorded, casts were removed and burrow volumes estimated by water displacement (Reynolds and Wakkinen 1987, Reynolds and Laundré 1988). Volume:length ratios were calculated and used as relative indices of burrow diameter to distinguish among different length-diameter ratios (e.g., long-narrow vs. short-wide burrows) within a species. The complexity of burrows was calculated as the length of a line connecting the two most distant points of the burrow divided by the burrow's total length. This index is 1.0 for linear burrows and progressively less with increased burrow complexity. This technique was found superior to other "indices of linearity" (Reichman et al. 1982, Cameron et al. 1988) that approached infinity for the short, relatively linear burrow systems found in this study. Additionally, the five burrow characteristics measured were used to generate z-score standardized principal component scores for the burrows of each species. The first principal

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[illegible]

TABLE 1. Means of measurements (± SD) recorded for burrows examined in this study. The lower portion of the table contains eigenvector coefficients for maximum depth (cm), volume (l), length (m), volume per length (vol/len), and complexity for the first (Z1-b) principal component from the principal component analysis of burrow characteristics. The percent variance (% var) explained by the principal component is also given.

Species	Depth	Volume	Length	Vol/len	Complexity	*n*
Pema[a]	19.2 ± 8.7	1.3 ± 0.9	0.7 ± 0.5	2.1 ± 1.1	0.8 ± 0.2	26
Dior[b]	40.9 ± 19.6	8.3 ± 8.7	2.7 ± 2.3	2.8 ± 0.8	0.6 ± 0.2	17
Mimo[c]	21.1 ± 6.6	1.8 ± 1.3	1.0 ± 0.6	1.8 ± 0.7	0.8 ± 0.2	42
Spto[d]	55.4 ± 36.6	10.2 ± 9.2	2.6 ± 2.5	4.1 ± 1.5	0.7 ± 0.2	19
Spel[e]	64.5 ± 36.2	12.4 ± 18.6	2.0 ± 1.9	5.3 ± 3.2	0.8 ± 0.2	

First principal component

Species	Depth	Volume	Length	Vol/len	Complexity	% var
Pema	0.35	0.57	0.55	0.05	−0.51	52.5
Dior	−0.08	−0.56	−0.54	−0.39	0.48	59.3
Mimo	−0.14	−0.68	−0.64	−0.19	0.27	39.2
Spto	−0.39	−0.58	−0.60	0.07	0.39	53.1
Spel	−0.36	−0.54	−0.52	−0.37	0.41	57.6

[a] Deermouse (*Peromyscus maniculatus*)
[b] Kangaroo rat (*Dipodomys ordii*)
[c] Montane vole (*Microtus montanus*)
[d] Townsend's ground squirrel (*Spermophilus townsendii*)
[e] Wyoming ground squirrel (*Spermophilus elegans*)

component score (burrow component, Z1-b) of a burrow was used to characterize a burrow system as a whole. Burrow components within a species were then used as the dependent variable in a multiple regression analysis with the first and second soil components. This analysis would help determine whether the burrow system as a whole was influenced by soil properties.

Ground squirrels construct "shallow" and "deep" burrows (Reynolds and Wakkinen 1987). To test for relationships between shallow or deep systems and soil types, we reanalyzed separately the maximum depth of the two system types for the two ground squirrel species. Shallow burrows for Townsend's ground squirrels were classified as being less than 60 cm deep (Reynolds and Wakkinen 1987). Based on an analysis of frequency distributions of maximum depth found in this study (unpublished data), Wyoming ground squirrel burrows less than 90 cm deep were classified as shallow systems. After the burrows were reclassified as shallow or deep, we found we had sufficient sample sizes to conduct only our regression analyses for shallow burrows.

Statistical comparisons were calculated with Statistics with Finesse® (J. T. Bolding, Box 339, Fayetteville, AR 72702), Biostatistics® ([illegible] Directory, 40 Glen Drive, Mill Valley, CA 94941), or Biostat® (Sigma Soft, 1430 Shalanwood Lane, Placentia, CA 92670) computer packages. All percent data were arcsine transformed before statistical calculations were made. The significance level was $P = .05$, and all reported means are ± standard deviation.

RESULTS

One hundred forty-nine burrow systems were excavated. Means and ranges of measurements recorded are presented in Table 1. Included in Table 1 are eigenvector coefficients for the first principal burrow components (Z1-b) for the five species. Except for montane voles, the first principal components explained 52–59% of the variance of the burrows sampled.

Bulk density and texture of soils at burrow sites varied among the five species and were quite variable within a species (Table 2). The first (Z1-s) and second (Z2-s) principal components of soils from burrow sites explained over 90% of the variance in samples for all five species (Table 2). Eigenvector coefficients for the equations describing the relationship among the soil properties for the first and second principal soil components are also presented in Table 1. For the first principal soil component equation within a species, bulk density and percent sand had the same sign (+ or −), which was opposite the signs for percent silt and clay.

TABLE 2. Means (± SD) and ranges of bulk density (g/cm³) and texture (% sand, % silt, and % clay) for [illegible] burrow sites. Texture values are untransformed. The lower portion of the table contains [illegible] for bulk density (BD) and percentages of sand, silt, and clay for the first (Z1-s) and second (Z2-s) principal components from the principal component analyses (PCA) of burrow site soils. The percent variance [illegible] for each principal component is also given.

Species	Bulk density	% sand	% silt	% clay	n
Pema[a]	1.36 ± 0.12	34.8 ± 11.5	51.5 ± 9.7	13.2 ± 4.7	15
range	1.12 – 1.50	20.8 – 51.2	31.8 – 62.8	5.5 – 19.8	
Dior[b]	1.28 ± 0.11	45.5 ± 8.9	38.5 ± 6.1	15.7 ± 7.0	4
range	1.15 – 1.48	23.9 – 55.2	25.0 – 46.7	5.6 – 27.8	
Mimo[c]	1.38 ± 0.22	40.8 ± 19.1	47.2 ± 16.4	12.2 ± 5.5	42
range	0.95 – 1.79	15.3 – 71.8	21.2 – 75.0	4.0 – 25.9	
Spto[d]	1.46 ± 0.21	60.3 ± 12.5	32.7 ± 9.5	6.4 ± 4.1	17
range	1.22 – 2.02	37.9 – 73.2	22.7 – 53.9	2.6 – 14.4	
Spel[e]	1.21 ± 0.18	42.5 ± 17.0	45.9 ± 15.0	11.4 ± 4.9	45
range	0.87 – 1.75	9.5 – 67.4	25.3 – 75.9	1.9 – 25.8	

	First principal component					Second principal component				
Species	BD	Sand	Silt	Clay	% var	BD	Sand	Silt	Clay	% var
Pema	+0.01	+0.65	−0.58	−0.49	58.8	+0.82	+0.07	−0.50	+0.48	11.2
Dior	−0.54	−0.61	+0.35	+0.47	62.4	−0.05	+0.69	−0.79	+0.61	28.1
Mimo	−0.49	−0.57	+0.55	+0.36	73.7	+0.48	−0.10	−0.22	+0.84	21.7
Spto	+0.42	+0.55	−0.52	−0.50	78.6	+0.88	−0.29	+0.39	+0.02	11.8
Spel	−0.12	−0.67	+0.64	+0.35	54.5	+0.75	−0.01	0.21	+0.65	30.7

[a] Deermouse (*Peromyscus maniculatus*)
[b] Kangaroo rat (*Dipodomys ordii*)
[c] Montane vole (*Microtus montanus*)
[d] Townsend's ground squirrel (*Spermophilus townsendii*)
[e] Wyoming ground squirrel (*Spermophilus elegans*)

Of the 28 multiple regression analyses of burrow characteristics with the first and second principal soil components, five were significant (Table 3). Four of the five significant multiple regressions were for characteristics of Wyoming ground squirrel burrows. Coefficients of determination for these four significant multiple regressions ranged from 17% for maximum depth of shallow burrows to 27% for maximum depth of all burrows combined (total depth). For these five significant multiple regressions, the only partial regression coefficient for the first principal soil component that was not significant was for total maximum depth (Table 3). In addition to significant multiple regressions, partial regression coefficients of the first principal soil components were significant for volume per length and complexity. Partial regression coefficients of the second principal soil components were significant only for total maximum depth, shallow maximum depth, and length of burrows (Table 3).

For Wyoming ground squirrels, the multiple regression coefficient for the first principal burrow component (Z1-b) was also significant (Table 3). Of the two independent variables, only the first principal soil component (Z1-s) had a significant partial regression coefficient. There was an inverse relationship between Z1-b and Z1-s, and the regression equation explained 16% of the variability seen in Z1-b (Fig. 1).

The fifth significant multiple regression was for depth of montane vole burrows. The coefficient of determination for this multiple regression was 16% (Table 3). Partial regression coefficients for both independent variables (Z1-s and Z2-s) were significant and negative. The regression equation for depth on Z1-s explained most (10%) of the variability seen in depth of microtus burrows (Fig. 2a). The partial regression coefficient of the first principal soil component was also significant for the volume-length ratios of microtus burrows. The regression coefficient was positive

TABLE 3. Results of multiple linear regression analyses between burrow characteristics, including the first principal burrow component (Z1-b), and the first two principal components for burrow site soils for the five species examined. Only regressions that were statistically significant are presented. Coefficient of determination (r^2), results of significance tests (F), and probability (P) are given for each multiple regression analysis. Significance values of partial regression coefficients for the principal soil components are also presented. Signs in front of t values indicate direction of the regression relationship.

	Multiple regression			Partial regressions				
				First component		Second component		
	r^2	F	P	t	P	t	P	n
Deer mice								
Volume	.25	2.03	.17	+0.56	.36	+1.94	.04	15
Length	.24	1.72	.22	+0.54	.37	+1.71	.05	14
Z1-b	.38	3.43	.07	+0.32	.50	+2.55	.01	14
Kangaroo rat								
Volume	.31	2.12	.13	+2.08	.03	+0.70	.29	14
Length	.40	3.63	.06	+2.56	.01	+0.85	.35	14
Z1-b	.33	2.21	.16	−1.81	.05	−1.06	.17	12
Townsend's ground squirrel								
Volume	.34	3.04	.08	+0.99	.41	+2.44	.02	15
Wyoming ground squirrel								
Depth								
Total	.27	5.97	.01	−0.87	.37	+3.43	.001	35
Shallow	.17	3.35	.05	+2.02	.02	−1.66	.05	36
Volume	.23	5.67	.01	+3.26	.001	+1.00	.18	40
Length	.19	4.84	.01	+2.15	.02	+2.25	.01	45
Vol/Len	.10	2.04	.14	+1.79	.04	−0.85	.36	40
Complexity	.08	1.61	.21	−1.81	.04	+0.01	.89	45
Z1-b	.18	1.13	.02	−2.73	.005	−0.96	.42	41
Montane voles								
Depth	.16	3.62	.04	−2.08	.02	−1.70	.05	42
Vol/Len	.13	2.67	.08	+2.03	.02	+0.92	.39	39

and the regression equation explained 11% of the variability in the data (Fig 2b).

None of the multiple regression coefficients for burrow characteristics were significant for kangaroo rats, deer mice, or Townsend's ground squirrels. However, partial regression coefficients for the first principal soil components were significant and positive for volume and length of kangaroo rat burrows (Table 3). Regression equations explained 27% of the variability in volume (Fig. 3a) and 36% of the variability in length of kangaroo rat burrows (Fig. 3b). Partial regression coefficients for the first principal soil component (Z1-s) and the first principal burrow component (Z1-b) for this species were also significant but negative. The regression equation for Z1-b on Z1-s explained 25% of the variability in the data (Fig. 3c).

For deer mice, partial regression coefficients for the second principal soil component (Z2-s) were significant and positive for volume and length of burrows and for the first principal burrow component (Table 3). Coefficients of determination were 0.23 for volume (Fig. 4a) and 0.22 for length (Fig. 4b). The regression equation for Z1-b on Z2-s explained 38% of the variability in the data (Fig. 4c).

For Townsend's ground squirrels, the only significant partial regression coefficient was for burrow volume on the second principal soil component (Table 3); the regression equation explained 28% of the variability (Fig. 1).

DISCUSSION

Our results indicate that differences in soil properties have different effects on the species of small mammals studied. Townsend's ground squirrels seemed the least affected by soil differences. For this species, only volume was significantly related to the second principal soil component. The second

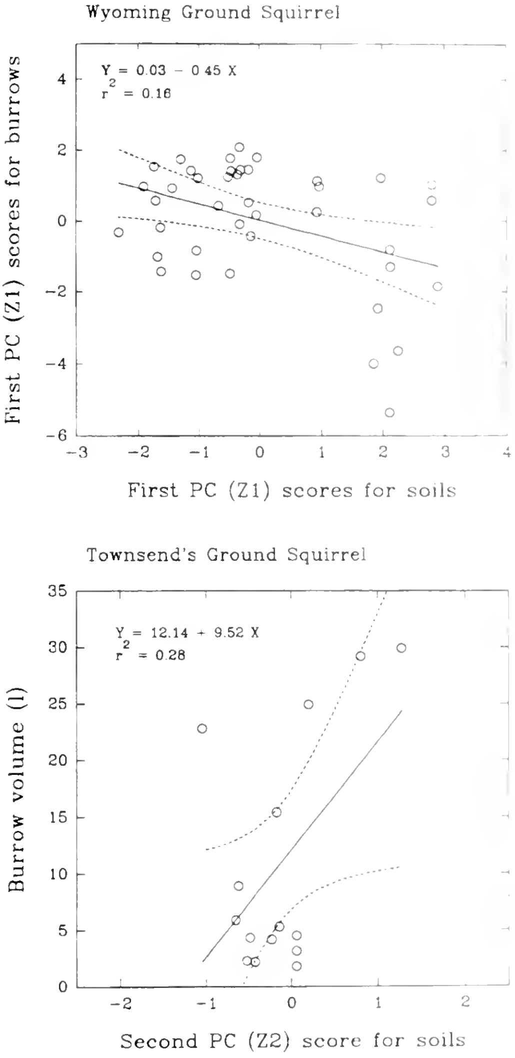

Fig. 1. Regressions, with 95% confidence intervals, of the first principal burrow component scores on the first principal soil component scores for Wyoming ground squirrel burrows, and of burrow volume on the second principal soil component scores for Townsend's ground squirrel burrows. All principal component scores are z-score standardized.

principal soil component was influenced positively by bulk density and percent silt and negatively by percent sand (Table 2). Thus, Townsend's ground squirrels constructed larger burrows in the firmer loamy soils. Reynolds and Wakkinen (1987) found significant regression relationships for this species among soil texture components and burrow depth, length, and volume. However, they used individual soil separates (percent sand, silt, and clay) in their analysis. As percent sand, silt, and clay are highly correlated, their use could bias the results of a regression analysis and account for the different findings between the two studies.

Fig. 2. Regressions, with 95% confidence intervals, of burrow depth (a) and volume per length (l/m) ratio (b) on the first principal soil component scores for montane vole burrows. All principal component scores are z-score standardized.

For kangaroo rats, burrow length and volume seemed directly influenced by the percentage of silt and clay in the soil. There was a significant negative regression of the first principal burrow component (Z1-b) on the first principal soil component (Z1-s) (Table 5). The magnitude of the first principal soil component is directly related to percent silt and percent clay and inversely related to percent sand and bulk density (Table 2). The first principal burrow component is inversely related to all burrow measurements except complexity (Table 1). However, a decrease in the complexity index indicates more complex burrows. Of the measurements, burrow depth

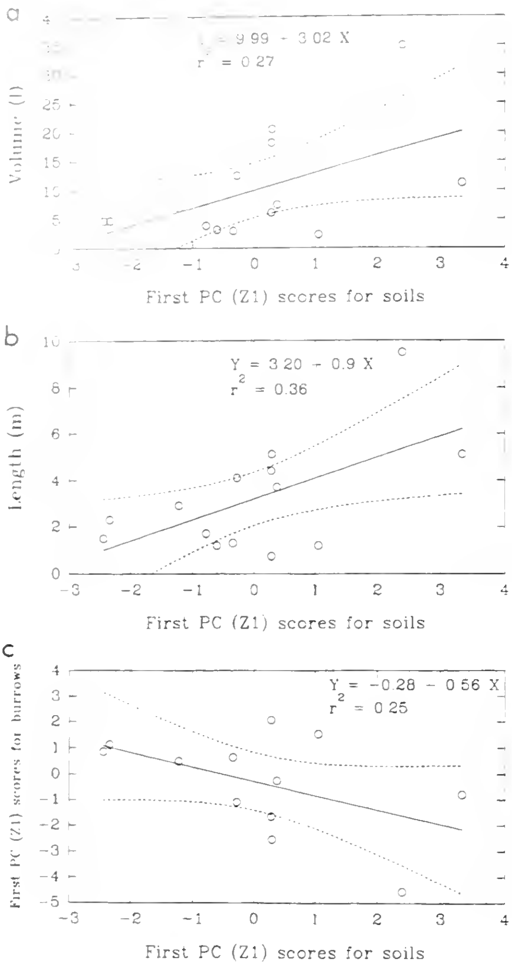

Fig. 3. Regressions, with 95% confidence intervals, of volume (a), length (b), and first principal burrow component scores (c) on the first principal soil component scores for kangaroo rat burrows. All principal component scores are z-score standardized.

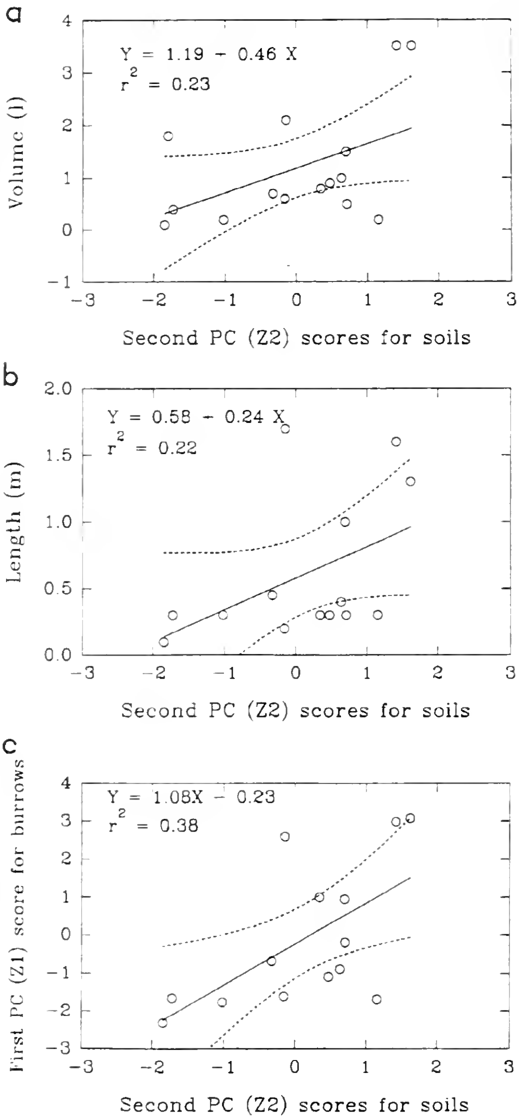

Fig. 4. Regressions, with 95% confidence intervals, of volume (a), length (b), and first principal burrow component scores (c) on the second principal soil component scores for deer mice burrows. All principal component scores are z-score standardized.

contributes little. Consequently, as the percentages of silt and clay increase (high Z1-s), burrows do not become much deeper but [illegible] do become longer and more complex ([illegible] complexity index), resulting in greater [illegible] soil being removed (low Z1-b). [illegible] interpretation is supported by the significance [illegible] partial regression coefficients for burrow volume and length [illegible] soil component (Table 3). [illegible] (1987) did not find a[illegible] hip between burrow cha[illegible] ture for this species. A[illegible] analysis likely accounted [illegible] ngs.

Several deer mice burrow characteristics, including the first principal burrow component, seemed to be influenced by soil properties as expressed by the second rather than the first principal soil component. For deer mice, the magnitude of the second principal soil component (Z2-s) increases as percent clay and bulk density increase or percent silt decreases; percent sand does not appear to influence this second soil component (Table 2). Relative to the first principal burrow component (Z1-b), all burrow measurements except complexity increased with higher component scores (Table 1). However, volume/length measurements did not contribute substantially to the score. Consequently, deer mice constructed deeper, longer, and more complex burrows (high Z1-b) in soils with higher bulk densities and percent clay (high Z2-s).

Burrowing behaviors of Wyoming ground squirrels seemed the most affected by differences in soil properties. Wyoming ground squirrel burrows had the most significant regression coefficients between characteristics and principal soil components. The first principal soil component (Z1-s) increased with increasing silt and clay and decreased with increasing bulk density and sand (Table 2). The first principal burrow component (Z1-b) was negatively related to all burrow properties except complexity (Table 1). As percent silt and clay increase (high Z1-s), all burrow characteristics increased (low Z1-b).

For montane voles, only depth and volume/length ratios of their burrows seemed influenced by soil properties. The first principal soil component was positively influenced by percent silt and clay and negatively related to percent sand and bulk density (Table 2). The relationship between depth and the first principal soil component was negative. Conversely, the volume/length ratio was directly related to the first principal soil component. Consequently, voles constructed deeper but narrower burrows in sandier but firmer soils.

In summary, five measurements supported the prediction that burrow characteristics are affected by soil properties. Most of these five characteristics were of Wyoming ground squirrel burrows, and we conclude that the burrows of this species are influenced in a predictable manner by the soil properties measured. Ten of the remaining burrow measurements were also significantly influenced by soil properties as described by individual principal soil components. We conclude that the remaining burrow measurements were not affected by soil attributes. Variability of these burrow properties is likely influenced by other, yet to be determined, factors such as length of occupancy or age and sex of occupant. To investigate the influence these factors may have on burrow structure and further delineate the impact of soil properties, we suggest that controlled experiments be conducted.

Our results suggest that soil characteristics of an area can affect various burrow dimensions in a predictive manner for the five small mammal species we studied. Soil effects on burrow structure could, in turn, influence the soil processes of that area. A difference in maximum depth of burrows changes the location of the reservoir of nutrients for recycling, increases the depth of soil aeration, and, especially in arid and semiarid areas, alters shallow subsurface water recharge patterns. Differences in volume, length, volume/length ratio, and complexity probably have a greater impact on the magnitude rather than the direction of the influence of a burrow on soil properties. For burrows of the same species with the same maximum depth, longer, larger, or more complex burrows within a given area would result in more surface soil deposition from, more aeration of, and more water infiltration to a given profile depth than shorter, smaller, or simpler burrows.

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MORPHOLOGY AND GROWTH VARIATIONS OF *AGROPYRON SMITHII* RYDB. (WESTERN WHEATGRASS) AT DIFFERENT SALINITY LEVELS

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ABSTRACT.—The purpose of this study was to determine the morphology and growth responses of *Agropyron smithii* Rydb. to various saline environments as evaluated in the laboratory. *Agropyron smithii* Rydb. (Rosana) seeds were germinated, transplanted into nutrient solutions with NaCl concentrations of 0, 50, 100, 150, and 200 mM, and grown for 80 days. Plant height, length of culm, and number of culms per plant were significantly reduced by the presence of NaCl in the nutrient solutions. As the external NaCl concentrations increased, values of root and plant ratio and leaf dry/fresh mass ratio increased significantly; biomass decreased significantly. However, the stomatal density, number of leaves per culm, and ratio of leaf length to leaf width were not significantly affected by the presence of NaCl.

Key words: Agropyron smithii, *western wheatgrass, salinity, salt, morphology, sodium chloride, biomass, stomata, culm, leaf, root.*

Agropyron smithii Rydb. (western wheatgrass or bluestem wheatgrass) is a native grass of the northern Great Plains (Schultz and Kinch 1976). It is common in dry prairies, dry sagebrush deserts, foothills, and along ditch banks and roadsides in sandy to heavy soils (Cronquist et al. 1977, Great Plains Flora Association 1986). *Agropyron smithii* is a valuable forage crop because of its high soil-stabilizing potential, rapid and vigorous seedling development, high nutritive value, and ability to withstand grazing (Knipe 1973, Cronquist et al. 1977).

Agropyron smithii Rydb. has been examined widely for several decades primarily in studies concerning germination and soil-related growth factors. Environmental factors (light and temperature) influencing germination have been investigated by Plummer (1943), Delouche and Bass (1954), Delouche (1956), Knipe (1973), Bokhari et al. (1975), Schultz and Kinch (1976), Toole (1976), and Sabo et al. (1979). The effects of day length and temperature on flowering and growth have been studied by Benedict (1940). The effects of topography, soil texture, and soil moisture on the distribution of *A. smithii* in the Arapaho Prairie (Arthur County, Nebraska) have been studied by Barnes and Harrison (1982). However, research concerning morphology and growth responses of this plant to salinity is very limited. Since *A. smithii* is a valuable grazing species in the arid West, it is often sought out for revegetation of these soils. A study of the morphology and growth responses of this species in saline environments may serve to help determine how this species adapts to saline soils.

The purpose of this study was to characterize the morphology and growth variations of *A. smithii* grown under different saline water culture conditions. Morphological variations that were examined include number of stomata per unit area, culm length, number of culms per plant, plant height, ratio of leaf length to width, and number of leaves per culm. Growth variations include fresh mass and dry mass of the whole plant, ratio of root to plant, and ratio of leaf dry mass to fresh mass.

MATERIALS AND METHODS

Thirty grams of *A. smithii* seeds (Rosana, lot number WR-1059) obtained from Sharp Bros. Seed Co. (101 E. 4th St. Rd., Greeley, Colorado) was germinated in moist vermiculite (15 C for 20 h and 30 C for 4 h per day) in complete darkness for 5 days. The seeds were held in darkness (15 C) for 5 days and then placed at alternating temperatures (28 ± 2 C) for a 12-h day and at 15 C for the 12-h night (as recommended by Toole 1976).

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A nutrient solution modified from Arnon and Hoagland (1940) was used in this study (Table 1). One-liter plastic containers were used to hold the experimental plants and the nutrient solutions. Square cardboard covers to support the plants were prepared with five equally spaced holes and impregnated with paraffin. Both covers and beakers were sterilized with a 5% Clorox solution before use.

When the *A. smithii* seedlings were 15 days old (2–3 cm long), they were placed through holes in the cover. Roots of the seedlings were bathed in the nutrient solution while shoot portions were supported in the cover holes with loose wads of cotton wrapped around each stem. Four plants were placed in each container. The hole in the center of the cardboard was for aeration. Each container was aerated for 30 min each 24-h period. For the first 9 days after transplanting, damaged or infected seedlings were replaced with fresh ones.

To allow the plants to acclimate to the saline culture media without excessive mortality, salinization of the medium began 9 days after the seedlings had been transferred to the nutrient solution. This was done by increasing the NaCl concentration in the culture solutions at the rate of 25 m*M* every four days to the final concentrations of 50, 100, 150, and 200 m*M*. Plants grown in unsalted cultures were used as controls. The nutrient solution was changed every 12 days during the experiment.

The experiments were carried out in a Sherer Gillette plant growth chamber (Model 512 CEL). Plants were grown under a 12-h day at 28 ± 2°C with humidity of 40 ± 5% and a 12-h night at 15°C with humidity of 60 ± 5%. Light was supplied by 12 cool white VHO fluorescent bulbs. Containers were placed randomly in the growth chamber. There were 80 plants (20 containers) for each treatment. All plants in each treatment were numbered. Data collection began when the plants were 80 days old. A subsample of 10 plants was measured for each treatment. Plants were selected for measurement without regard to container by picking numbers from a table of random numbers. It was possible that more than one plant per container [illegible] treatment. This may have [illegible] differences in plant [illegible] among containers.

Table 1. Composition of the nutrient solution modified from Arnon and Hoagland (1940).

Salt	g/L
KNO_3	1.02
$Ca(NO_3)_2 \cdot 4\,H_2O$	0.71
$NH_4H_2PO_4$	0.23
$MgSO_4$	0.24
Salt	**mg/L**
H_3BO_3	2.86
$MnCl_2 \cdot 4\,H_2O$	1.81
$CuSO_4 \cdot 5\,H_2O$	0.08
$ZnSO_4 \cdot 7\,H_2O$	0.22
$H_2MoO_4 \cdot H_2O$	0.09
$FeSO_4 \cdot 7\,H_2O$ 5 g/L & tartaric acid 4 g/L	0.6 m*L*/L (every 4 days)

Morphological Measurements

The number of stomata per mm^2 was determined by obtaining stomatal peels made by applying a thin layer of AB Dick mimeograph correction fluid on the center (abaxial surface) of a leaf and allowing it to dry. Using double-sided Scotch tape, we removed the peel and placed it on a microscope slide. Counts were made at a magnification of 200X by using a calibrated ocular grid (Antlfinger 1981). The second leaf from the top of a randomly selected plant was used for this count. Culm length was determined by measuring from the cardboard to the top node. Plant height was determined by measuring the full length of the plant above the cardboard (including leaf). Leaves longer than 3 cm were counted to determine the number of leaves per culm. The third leaf from the top was chosen for leaf length and width ratio measurement. The reading for leaf width was taken from the widest part of the leaf. If a plant had more than one culm, the longest one was chosen for all of the above measurements.

Growth Measurements

Plants were harvested when they were 80 days old. Growth of the plants was determined by first measuring fresh mass and then dry mass following a drying period of 72 h at 105°C. The aboveground and belowground (above cardboard and below cardboard) dry masses were measured separately for determining root/plant ratios. For measurements of leaf dry and fresh mass ratios, all fresh leaves collected from a randomly selected plant were

TABLE 2. Morphological variation of *A. smithii* grown in nutrient solutions [illegible] NaCl [illegible]. Values represent mean (*n* = 10) ± one standard deviation. Significance level [illegible] ANOVA.

Character	Treatments (mM NaCl)					
	0	50	100	150	200	[illegible]
Stoma # mm² leaf	56 ± 9.5	56 ± 8.2	58 ± 9.8	[illegible]	[illegible]	[illegible]
Culm # plant	14 ± 4.7	5 ± 1.2	4 ± 1.0	2 ± 0.7	2 ± 0.7	[illegible]
Leaf # plant	5 ± 0.7	5 ± 0.7	[illegible]	[illegible]	[illegible]	[illegible]
Culm length cm	19 ± 4.9	13 ± 2.8	14 ± 4.2	10 ± 2.0	8 ± [illegible]	[illegible]
Plant height cm	52 ± 5.0	40 ± 6.9	37 ± 4.8	[illegible]	27 ± [illegible]	[illegible]
Leaf length cm	31 ± 3.8	26 ± 5.9	25 ± 5.1	21 ± 5.5	16 ± 4.7	[illegible]
Leaf width cm	0.5 ± 0.06	0.47 ± 0.06	0.44 ± 0.05	0.37 ± 0.05	[illegible]	[illegible]
Leaf length width	63 ± 9.9	50 ± 13	51 ± 7.7	60 ± [illegible]	66 ± [illegible]	[illegible]

weighed and then placed in an oven for 72 h at 105°C.

One-factor ANOVA was used to determine significant differences (α = .05) among different treatments. The one-factor ANOVA test used procedures outlined by Kleinbaum et al. (1988).

RESULTS

Morphological Measurements

The number of stomata from plants grown in the five different nutrient solutions did not change as the external sodium chloride concentrations increased (Table 2). The number of culms per plant decreased as the external sodium chloride concentrations increased. The number of leaves per culm was not affected by the external sodium chloride concentrations. Length of culms and height of plants decreased as concentrations of sodium chloride in nutrient solutions increased. Generally, plants that had a longer culm also had a greater plant height (Table 2). Leaf length and width decreased as external sodium chloride concentrations increased. However, the ratio of leaf length to leaf width was not affected by external sodium chloride concentrations (Table 2). External sodium chloride reduced leaf size and did not affect leaf shape.

Growth Measurements

Growth of *A. smithii* as measured by dry mass and fresh mass was inhibited by the presence of sodium chloride in nutrient solutions. Size reduction was most obvious when the 0 m*M* and 50 m*M* sodium chloride treatments were compared. As salt concentrations increased above 50 m*M*, dry and fresh mass differences between two adjacent treatments became less obvious (Table 3). Growth of the shoot was more sensitive than the root to sodium chloride. Plants grown in solutions with higher concentrations of sodium chloride had higher root plant ratios (Table 3). To determine leaf succulence, the ratio of leaf dry mass and fresh mass was measured. Mean dry fresh mass ratios increased slightly with an increase in external sodium chloride concentrations (Table 3). Thus, external sodium chloride did not stimulate succulence of *A. smithii* leaf tissue.

DISCUSSION

Morphological Measurements

The number of stomata per unit area was not significantly influenced by the presence of NaCl. This finding agrees with a previous study of *Borrichia frutescens* by Antlfinger (1981). It is apparent that *A. smithii* does not reduce transpiration by decreasing stomata unit area to cope with water stress resulting from the presence of NaCl in nutrient solutions. However many plants in high-light and low-humidity environments such as deserts reduce tranpiration by lowering their stomatal index to cope with water stress (haven et al. 1981).

The number of leaves per culm of *A. smithii* was not affected by increasing salt concentration. This unexpected result does not agree with findings in *Oryza sativa* [illegible] (Yeo and Flowers 1984) and in *Borrichia frutescens* (Antlfinger 1981). Yeo and Flowers (1984) reported that in saline habitats the reduction of leaf number per culm in *O. sativa* was the result of an increase in leaf death rate

TABLE 3. Size variation of *A. smithii* grown in nutrient solutions with five different NaCl concentrations. Values represent mean (*n* = 10) ± one standard deviation. Significance levels are for the F-tests from the ANOVAs. FM and DM represent fresh mass and dry mass, respectively.

Character	Treatments (m*M* NaCl)					Significance level
	0	50	100	150	200	
FM (g/plant)	10 ± 1.1	2.5 ± 0.6	1.9 ± 0.3	1.1 ± 0.24	0.9 ± 0.24	.0001
DM (g/plant)	2 ± 0.23	0.6 ± 0.12	0.54 ± 0.09	0.31 ± 0.05	0.27 ± 0.06	.0001
Root/plant ratio	0.12 ± 0.02	0.13 ± 0.05	0.14 ± 0.06	0.18 ± 0.07	0.18 ± 0.05	.0228
Leaf DM/FM ratio	0.24 ± 0.03	0.26 ± 0.02	0.27 ± 0.03	0.28 ± 0.03	0.28 ± 0.02	.0036

and an unaltered production of new leaves. Yeo and Flowers (1982) also found that leaf sodium content of *O. sativa* increased as leaf age increased when this plant was exposed to saline environments. Early shedding of older leaves and young-to-old leaf gradients of sodium content permit younger leaves to remain at sublethal salt concentrations. So, reduction in the number of leaves per culm in saline environments for some species could be considered a survival factor. *Agropyron smithii* does not reduce the number of leaves per culm in saline environments and apparently does not use this means of survival. In contrast to *Oryza sativa*, Jefferies and Rudmik (1984) reported that in *Triglochin maritima*, which is a perennial species and widespread in saline and calcareous habitats, the death rate of leaves decreased in response to increased salinity. Further studies are needed to clarify the discrepant responses of this character to saline environments.

The number of culms per plant was significantly different among the five treatments (Table 2). Data obtained in this study support the hypothesis that salinity reduces vegetative organ numbers (Jefferies and Rudmik 1984). It appears that concentrations of NaCl above 50 m*M* do not have much additional negative impact on culm number in this species.

Sodium chloride had a negative impact on the length of culm and plant height of *A. smithii*. Responses of these two characteristics to salt are generally the same as those in *Borrichia frutescens* (Antlfinger 1981).

Leaf lengths and widths were significantly reduced by the presence of sodium chloride in culture solutions. Reduction of leaf growth by NaCl has also been found in some other plants such as *Phaseolus vulgaris* L. (Nieman and Poulsen 1971, Neuman et al. 1988), *Borrichia frutescens* (Antlfinger 1981), and *Triglochin maritima* (Jefferies and Rudmik 1984). One possible mechanism for NaCl inhibiting leaf growth is that reduction of water potential in the root zone causes reduction of turgor in leaf cells, thus reducing growth of the leaf. NaCl-induced reduction of turgor was found in seedlings of *Phaseolus vulgaris* L. grown in media with NaCl (Neumann et al. 1988).

Growth Measurements

Fresh mass and dry mass of *A. smithii* were significantly reduced by the presence of sodium chloride in the nutrient solutions. Reduction of plant size by sodium chloride has been found in a variety of plants such as *Cicer arietinum* (Lauter et al. 1981) and *Trifolium repens* (Smith and McComb 1981). Generally, NaCl reduces plant growth through (1) mineral competition, since it reduces the uptake and transport of nitrogen (Aslam et al. 1984), phosphate (Maas et al. 1979), potassium (Lynch and Läuchli 1984), and calcium (Lynch and Läuchli 1985); (2) toxic effects by reducing the photophosphorylation (Ball and Anderson 1986, Muller and Santarius 1978) and enzyme activity of RuBP carboxlase (Seemann and Critchley 1985); and (3) osmotic effects on water availability, which inhibit cell growth, cell-wall synthesis, protein synthesis, carbon assimilation and allocation (Cheeseman 1988), respiration (Glass 1988), and photosynthesis (Black and Bliss 1980).

High salt does not reduce the value of the dry/fresh mass ratio of leaf tissue (Table 3). That NaCl does not induce *A. smithii* leaf succulence does not agree with the findings on *Phaseolus vulgaris* L. (Seemann and Critchley 1985), *Borrichia frutescens* (Antlfinger 1981), and *Atriplex patula* (Longstreth and Nobel 1979). Tissue succulence can prevent the intracellular NaCl concentrations from becoming excessively high (Lüttge and Smith 1984). It appears that *A. smithii* uses some other mechanism to tolerate the high concentration of NaCl within cells. Glass (1988) reported that halophytes sequestered NaCl within the vacuoles and that the cytoplasmic phase was maintained isoosmotic within the vacuole by means of noninjurious organic solutes such as glycerol, sucrose, amino acids (particularly proline), mannitol, and various other N-containing derivatives. Further study is needed to identify how *A. smithii* tolerates high intracellular NaCl concentrations.

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COMPARISON BETWEEN PLANT SPECIES IN BUSHY-TAILED WOODRAT MIDDENS AND IN THE HABITAT

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ABSTRACT.—Bushy-tailed woodrats (*Neotoma cinerea*) collect vegetation and store it in middens. We asked to what extent plant species collected by woodrats reflect the array of species growing in the habitat. Species composition of plant clippings at 20 bushy-tailed woodrat middens in central Colorado was compared to vegetation growing within 30 m of the dens. Amount of overlap between midden and habitat species was low (28–49%) when all taxa were included; however, if only woody taxa were considered, overlap was 71–89%. Sorensen's Index of Similarity exhibited a like pattern; the index increased markedly if only woody taxa were included. Only one plant species not found within 30 m of a den occurred in significant amounts in the middens. Bushy-tailed woodrats collected a wide array of species but were more selective the greater the habitat plant diversity. Results of this and other studies indicate that the concordance between midden contents and habitat vegetation decreases with increasing habitat plant diversity. Ancient woodrat middens are nonetheless useful to paleontologists seeking to reconstruct past vegetation associations since woody vegetation is well represented in middens.

Key words: bushy-tailed woodrat, Neotoma cinerea, *midden, foraging, paleoecology, fossil midden.*

The bushy-tailed woodrat, *Neotoma cinerea*, occurs in western North America in a wide range of habitats and temperature regimes. In Colorado, *N. cinerea* most often lives in shrub and woodland communities where Douglas fir, ponderosa pine, aspen, and a variety of shrubs such as sagebrush, snowberry, rabbitbrush, and scrub oak occur. However, the bushy-tailed woodrat is more dependent on the existence of suitable crevices in cliff outcrops than on the type of vegetational association (Finley 1958). The woodrat constructs its nest in such a crevice, wherein it typically accumulates a separate midden consisting chiefly of bones, fecal pellets, woody branches, and plant clippings. Separate food caches may be nearby. Clippings consist of either vegetation stored for future consumption or debris remaining after partial consumption by a woodrat at the den.

We investigated species composition of plants collected by bushy-tailed woodrats in Colorado at elevations of 2400 and 2530 m. Sites included different vegetational associations ranging from xeric to dry-mesic. The occurrence of individual plant species in middens, nests, and food caches was compared to the presence of each species growing within 30 m of the cliff. This comparison is of interest for several reasons. First, paleontologists use contents of fossil woodrat middens to determine species composition of Pleistocene and early Holocene vegetational communities (Betancourt et al. 1990). It is therefore important to know whether woodrats collect plant material based on availability (cf. Wells 1976), or whether woodrat selectivity introduces a significant bias in species composition of midden deposits (cf. Dial and Czaplewski 1990). Second, little is known about the behavioral ecology of bushy-tailed woodrats. Analysis of these midden contents provides information on the foraging and collecting behavior of *N. cinerea* in habitats differing in plant diversity and species composition. Third, midden contents may mirror woodrat diets. Dial (1988), in a study of *N. albigula*, *N. devia*, and *N. stephensi* in a shrub-steppe juniper woodland ecotone, determined that plant clippings at middens did reflect the diet of those woodrat species, although the two were not strongly correlated.

We asked the following question: To what extent do the species collected by bushy-tailed woodrats and deposited in the den area represent the availability of plant species in the habitat? Our results also provided information on distances traveled by foraging bushy-tailed woodrats. Diet per se will not be discussed here.

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Study Area

Three sites in Gunnison County, Colorado, were studied. Robert B. Finley conducted woodrat studies at these cliffs nearly 40 years ago (Finley 1958). Finley IA and Finley IB are different walls of a rock outcrop that forms a small canyon. The canyon is located 4.5 km north of Almont on the east side of Colorado State Highway 135 at an elevation of 2530 m. Finley IA has a western exposure and IB faces south. The cliffs are composed of sandstone with granite caps. The nearly level cliff top is sparsely vegetated compared to the area below the cliffs. Spruce (*Picea pungens*) and aspen (*Populus tremuloides*) are common below Finley IA cliff, and the area at the base of Finley IB cliff is a sagebrush and mixed-shrub community with few trees.

The third site, Finley II, is 1.7 km south of Almont along Highway 135 at an elevation of 2400 m. The cliff has an eastern exposure and, like Finley I, is sandstone. Finley II is in a juniper/sagebrush community that includes yucca, cactus, and a variety of shrub species. The vegetation on top of and below the cliff is similar. Finley II is the most xeric of the three sites.

These sites were chosen because they differed in vegetational composition and because live-trapping confirmed the presence of resident *N. cinerea* populations.

Methods

Bushy-tailed woodrats do not live in middens themselves, and the study site middens tended to be diffuse and shallow, and were unindurated; food caches were small, discrete piles on rock or sandy soil. From 1 July through 15 August 1986, all plant clippings found on the surface of middens, in nearby food caches, and in the nests (not including the nest material) were identified. In all but a few instances identification of plant fragments was possible at the site. For brevity, we will refer to all clippings from middens, caches, and nests as being from middens. Fragments from 20 middens were examined.

We were unwilling to permanently remove den material for sifting or sorting due to an ongoing woodrat behavior study. This may have introduced a source of bias, since small (<5 mm in length) plant fragments may have fallen into the loose debris pile of a midden and not been recorded. However, virtually all fragments in food caches and nests were accessible, and some seeds and fine material were recovered from middens with our protocol.

Vegetation near the cliffs was sampled during the second and third weeks of August and was divided into three categories: (1) herbaceous plants, including cacti; (2) shrubs; (3) trees, including saplings (diameter at breast height <2.5 cm). Botanical nomenclature follows that of Weber (1976) and Barrell (1969).

All trees and shrubs within 30 m of the cliff face at each site were included. Tree basal area and shrub canopy were calculated. Herbaceous species within 30 m of the cliff edge were sampled using 0.1-m^2 quadrats that were placed by drawing numbers randomly and pacing off the appropriate distances. The minimum number of quadrats needed to adequately survey the community was determined by constucting a species-area curve. Individual plants were counted except for clonal species such as the grasses and *Antennaria*, *Arctostaphylos*, and *Selaginella*, for which the percentage of groundcover was estimated. All species recorded in the middens and the habitat are listed in Appendix 1 and 2.

Results

One measure of concordance between midden contents and species in the habitat is the percentage of taxa they have in common. When vegetation was divided into categories of woody (trees, shrubs) and herbaceous (forbs, grasses) species, shared taxa ranged from 0 to 100% (Table 1). Woody species in the habitat were better represented in middens than were herbaceous species, and at two sites there was a greater overlap among trees than among shrubs (Table 1).

When all taxa were pooled, overlap at the three sites ranged from 27.8% at Finley IA to 48.5% at Finley II (Table 2). Removing grasses from the calculation increased the percent overlap, and when only woody species were included, overlap increased markedly at all sites (Table 2).

Sorensen's Index is commonly used to assess similarities between plants in woodrat middens and in the environment (Spaulding

TABLE 1. Number of plant taxa in the middens (numerator) versus the number of plant taxa in the habitat (denominator). Percent of shared taxa outside parentheses. *N* = number of middens examined

	Trees	Shrubs	Forbs	Grasses
Finley IA *N* = 6	75% (3/4)	75% (6/8)	20% (6/31)[a]	0% (0/12)
Finley IB *N* = 7	100% (3/3)[a]	64% (9/11)	36% (11/31)[a]	18% (2/11)
Finley II *N* = 7	100% (2/2)	86% (6/7)[a]	25% (4/16)	50% (4/8)

[a] One species in midden not found growing within 30 m of the cliff base. That species not included in the numerator.

et al. 1990). SI values were relatively low; if only woody species were considered, the similarity index was 80% or greater (Table 2). Regardless of which categories of plants were included in the calculation, the greater the number of taxa present, the lower the similarity index.

DISCUSSION

In the years since Wells (1976) proposed a connection between the wealth of plant macrofossils preserved in middens deposited by long-dead woodrats and ancient plant communities, many paleontologists have used fossil woodrat middens to reconstruct Pleistocene and Holocene vegetational associations and corresponding climates (e.g., Cole 1983, Cole and Webb 1985, Spaulding 1985). The validity of these reconstructions rests in large part upon the extent to which *Neotoma* middens contain an accurate representation of the surrounding vegetation.

The amount of overlap between taxa collected by *N. cinerea* and taxa growing in the vicinity (Table 2) was considerably lower than in other studies. Spaulding (1985) reported a 68–84% overlap for taxa growing within 30 m of an unspecified woodrat species' middens. Dial and Czaplewski (1990) indicated an average of 71.8% overlap for *N. albigula*, 45.8% for *N. devia*, and 53% for *N. stephensi*. If, for each of our sites, taxa that were uncommon and of low biomass in the habitat and taxa that appeared in only one midden and in low abundance were omitted from analysis, then overlap for Finley IA was 40%, Finley IB 53%, and Finley II 64%. Omitting rare taxa increases the degree of overlap, but still far fewer than three-quarters of the common plants in the vicinity appeared in the midden.

An average of 25% of all species present in *N. cinerea* middens were herbaceous (range for the three sites, 13.9–32.0%). There were few herbaceous perennials in the areas sampled by Spaulding (1985) and Dial and Czaplewski (1990). If herbaceous perennials are omitted from our *N. cinerea* data, the overlap increases from an average of 39.6% for all sites to an average of 78.2%. This latter percentage is comparable to Spaulding's results (1985) and those for *N. albigula* (Dial and Czaplewski 1990).

Other workers assessed the similarity between midden plant taxa and habitat plant taxa with Sorensen's Index. These similarity indices generally were greater than the 43–63% obtained from our *N. cinerea* data. Published similarity indices were 67–84% (Spaulding 1985), 80% (Cole and Webb 1985), 89% (Cole 1983), and 64–92% (Cole 1982) for unnamed *Neotoma*. Vaughan (1990) reported lower similarity indices and listed approximate values of 50% for *N. mexicana* and 30–40% for *N. lepida*, *N. albigula*, *N. stephensi*, and *N. devia*. If only woody taxa from the *N. cinerea* data are included, the range for the index is 80–89% (Table 2).

TABLE 2. (A) Percent of overlap between plant taxa present in middens and those present in habitat. (B) Similarity between plant taxa present in middens and those present in habitat as calculated with Sorensen's Index. SI = 2C/(A + B) where A = number of species in middens, B = number of species in habitat, and C = number of species in both middens and habitat. Total number of taxa in habitat: Finley IA, 54; Finley IB, 59; Finley II, 35.

	All taxa	Grasses omitted	Woody taxa
(A)			
Finley IA	27.8	35.7	75.0
Finley IB	42.1	47.9	70.6
Finley II	48.5	48.0	88.9
(B)			
Finley IA	42.9	50.8	85.7
Finley IB	58.1	60.5	80.0
Finley II	62.7	63.2	88.8

What conclusions can be reached from inspection of these data on different *Neotoma* species living in various vegetational communities? How accurately can the habitat vegetation be predicted by analysis of woodrat middens?

It should be noted that typical paleomiddens differ from the modern middens analyzed in this study. Nonindurated modern middens represent a shorter collection period than do ancient indurated ones. We have no way of assessing whether plant clippings we identified are an accurate sample of plant debris that would accumulate during several years. Relatively low frequency of grasses and forbs in *N. cinerea* middens could be a result of our overlooking small plant fragments that would be recovered in the sieving procedure used on paleomiddens. However, Dial and Czaplewski (1990) did not identify plant parts <3 mm in diameter; yet they reported an average overlap of 72% between modern middens of *N. albigula* and adjacent vegetation. And, as stated earlier, we did identify some small plant fragments in our middens, so a strong bias against grasses and forbs as a result of not including fine material does not alone explain the low overlap between these types of plants in the middens and in the habitat.

Plant species richness in the *N. cinerea* habitat was considerably greater (N = 33–59) than at other sites. For example, at Spaulding's (1985) sites, there were 14–19 taxa; Dial and Czaplewski's (1990) transects included 20 species plus several grasses. When the results of all studies were compiled, Sorensen's Index was, in general, negatively correlated with species diversity—the greater the habitat diversity, the lower the degree of concordance between midden contents and habitat. In diverse habitats then, the predictability of habitat vegetation from midden contents is reduced.

Different woodrat species exhibit different degrees of selectivity during collecting (Dial and Czaplewski 1990, Vaughan 1990). Dial's (1984) removal experiment showed that midden contents changed, sometimes drastically, following a change in the species of the den occupant. *N. cinerea* and *N. mexicana* are considered generalist collectors (Finley 1958, Vaughan 1990), whereas *N. stephensi* is a specialist and unquestionably its middens offer a strongly biased account of the vegetational community (Vaughan 1982). However, our *N. cinerea* data indicated that although *N. cinerea* midden contents include many plant species, less than 50% of the species within 30 m of the midden are represented. When considering all plant taxa, our *N. cinerea* middens are not very good predictors of the habitat vegetation. This is true in habitats of different levels of diversity, even though *cinerea* is among the most catholic collectors within the genus. In fact, bushy-tailed woodrats are more selective the greater the vegetational diversity.

If, however, paleontologists are primarily concerned with community type rather than specific floral components, woodrat middens probably are good predictors. There is strong concordance between the woody species collected by woodrats and the woody species found in the environment. Since communities with woody flora can be characterized in large part by which woody species are present (e.g., Engelmann spruce/subalpine fir forest vs. ponderosa pine forest), community type and associated climate can be ascertained using midden contents, as long as the species responsible for the midden is not one whose extreme selectivity introduces substantial bias.

Individual *N. cinerea* had home ranges much larger than 60 m in diameter (Frase unpublished data), but only three plant species present in middens did not grow within 30 m of the cliff edge. *Cirsium undulatum*, present in only small amounts in only one midden at each site, grew within 40 m of the cliff edge. A bit of *Juniperus scopulorum* was present in one midden at Finley IB. The only taxon that appeared in significant amounts in middens despite its absence close to the cliff was *Eurotia lanata*, winterfat, at Finley II. Winterfat was quite common 50 m and more from the base of the cliff. Thus, with one exception, our bushy-tailed woodrats need not travel more than 30 m from home to forage.

In general, most species of woodrats do not travel very far to forage (summarized in Finley 1990), and the bushy-tailed woodrats in this study conformed to that pattern. It is largely assumed that this behavior greatly reduces the risk of predation. Results of our midden analysis present an intriguing question we are currently investigating: If woodrats at our sites can satisfy their foraging needs within a 30-m radius of their dens, and if it is risky to travel away from the shelter of the cliff, then why, even outside of breeding season, do individuals regularly travel distances of 100–500 m from their dens?

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APPENDIX 1. Plant species found in bushy-tailed woodrat middens and habitat. M indicates present in midden. H indicates present in habitat.

	Finley 1A	Finley 1B	Finley 11
TREES			
Juniperus scopulorum	H	M	M H
Picea pungens	M H	M H	
Pinus ponderosa	M H	M H	
Populus tremuloides	M H	M H	
Pseudotsuga menziesii			M H
SHRUBS			
Amelanchier alnifolia		H	M H
Artemisia tridentata	M H	M H	M H
Chrysothamnus nauseosus		M H	
C. parryi	H	M H	
C. viscidiflorus	H	H	M H
Eurotia lanata			M
Holodiscus dumosus		M H	
Juniperus communis	M H	M H	
Pentaphylloides floribunda		H	
Purshia tridentata	M H	M H	
Ribes cereum	M H	M H	
Rosa woodsii	M H	M H	
Rubus idaeus		M H	
Symphoricarpos tetonensis	M H	H	M H
Tetradymia canescens	—		M H
Yucca glauca	—	—	M H

	Finley IA	Finley IB	Finley II
[illegible]			
[illegible]	H	M H	H
[illegible]	H	M H	H
[illegible]	H	M H	—
[illegible]	M H	M H	—
[illegible]	M H	M H	M H
[illegible]	M	M	M H
[illegible]	M H	M H	—
[illegible]	H	M H	—
[illegible]	—	M H	—
[illegible]	—	M H	—
[illegible]	—	—	M H
[illegible]	—	—	M H
[illegible]	M H	—	—
[illegible]	M H	M H	—
[illegible]			
[illegible]	—	H	M H
[illegible]	H	H	M H
[illegible]	H	M H	H
[illegible]	—	H	M H
[illegible]	H	M H	M

[illegible]

	Finley IA	Finley IB	Finley II
[illegible]			
[illegible]	—	H	H
[illegible]			
[illegible]	H	H	—
[illegible]	—	H	H
[illegible]	H	—	—
[illegible]	H	—	—

	Finley IA	Finley IB	Finley II
[illegible]	H	H	—
[illegible]	—	H	—
[illegible]	—	—	H
[illegible]	H	—	—
[illegible]	H	H	H
[illegible]	H	H	—
[illegible]	H	H	H
[illegible]	H	H	—
[illegible]	H	—	—
[illegible]	H	H	—
[illegible]	H	H	—
[illegible]	H	H	—
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[illegible]	H	H	H
[illegible]	—	H	—
[illegible]	H	—	—
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[illegible]			
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[illegible]	H	H	—
[illegible]	H	H	—

Great Basin Naturalist [illegible]

LONG-TERM FLUCTUATIONS OF AN ISOLATED POPULATION OF THE PACIFIC CHORUS FROG, *PSEUDACRIS REGILLA* IN NORTHWESTERN NEVADA

Norman H. [illegible]

ABSTRACT.—In [illegible] metamorphosis and [illegible] annihilated chorus frogs in the [illegible] *Pseudacris regilla*, the Pacific [illegible] became reestablished after [illegible] drastic rises in water temperature [illegible] green with black dorsal speckles [illegible] restrial garter snake *Th*[illegible]

Key words: *Pacific* [illegible] *predators*.

Pseudacris regilla (= *Hyla regilla*), the Pacific chorus frog, is one of the most abundant and widespread amphibians in the northwestern Nevada portion of the Great Basin. Yet, no studies have been published on the chorus frog in this geographical area. Test (1898), Van Denburgh and Slevin (1921), and Cowles and Bogert (1936) reported that chorus frogs in southern Nevada were localized and not especially abundant. Linsdale (1940) recorded *P. regilla* populations in southern Nevada. Banta (1961) studied populations of *P. regilla* along the lower Colorado River in southeastern Nevada and assumed other established populations were exterminated by the rising waters of Lake Mojave. Outside the Great Basin, Brattstrom and Warren (1955) made observations on the ecology and behavior of the Pacific chorus frog in southern California. Jameson (1956, 1957) reported on the growth, dispersal, survival, population structure, and homing responses of the Pacific chorus frog in the Willamette Valley, Oregon. Whitney and Krebs (1975) studied the spacing and calling in Pacific chorus frogs at Marion Lake, British Columbia. Reynolds and Stephens (1984) reported on multiple ectopic limbs in a wild population of *P. regilla* near Boise, Idaho.

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[1] [illegible]
[2] [illegible]

juniper on the north, east, and south sides of the canyon that contain the pond. To the west along the canyon are dense growths of Fremont cottonwood (*Populus fremonti*), black willow (*Salix nigra*), and white clover (*Trifolium repens*).

METHODS

From 1974 to 1989 censuses of chorus frogs in or near the pond were conducted on alternate evenings from 1600 to 2300 PST throughout the breeding season, which extended from February to April. During the remaining nine months of the year, periodic counts of adult frogs were made.

Each census was conducted from an observation site located 6 m from the pond. From this point the total number of frogs in or near the entire pond was counted. To increase the accuracy of the counts, the pond was divided into four regions: northeast, northwest, southeast, and southwest. Each census started with the northeast region. After all frogs were counted in this region, counts were then made in northwest, southeast, and southwest sections. To increase the accuracy of the counts, a spotlight and binoculars were used. The procedure used to conduct a census was the same each year of the study.

In addition to conducting annual population censuses, we also recorded life history information. For each year of the study the date was recorded for the following activities: entering pond, chorusing, mating, egg laying, hatching, exiting of adults, completion of metamorphosis, and exiting of juveniles.

Throughout the study, air temperature was recorded 1 m above the ground and 3 m north of the pond, and water temperature was taken at the center of the pond at a depth of 15 cm.

Information concerning the study area, pond, and chorus frogs from 1905 to 1978 was provided by Mrs. George Minor.

RESULTS

Migration to the Pond

Migration of chorus frogs to the pond was documented to 1905, and it probably occurred many years prior to that (Mrs. Minor personal communication).

Except for flood years, a few male chorus frogs migrated to the pond in late February from 1975 to 1989. These males produced a chorus that attracted other males. The number of males increased from a few in late February to an average of 25 in mid-March. From mid-March to late April the number of males decreased to fewer than 5. In addition to attracting males, the chorus appeared to attract females. The breeding population of males and females peaked in March (mean ± SD, 60 ± 3.8; range, 53–66; Fig. 1 and Table 1). Thus, chorus frogs migrated to the pond from late February to early May, and the male breeding chorus extended over a 3-month period.

Reproduction and Metamorphosis

Mating commenced soon after the frogs entered the pond and continued until early April. During this time no territorial disputes or fighting was observed. Egg laying occurred from mid-March to mid-May; eggs began to hatch into tadpoles in mid-April. The brownish black tadpoles tended to localize in the deeper (up to 1.2 m), downstream portion of the pond. Tadpoles and near-transformed individuals grew rapidly in the 12–18° C water, and by early October all frogs gradually exited the pond. From early October to February only an occasional chorus frog was seen or heard in the pond. The transformed individuals probably matured in one season and returned to the pond as fully grown adults the next year as shown by Jameson (1956).

Ninety percent of transformed adults were light to dark green with dorsal black speckles and black eye stripes. Brattstrom and Warren (1955) found that green and brown phases occurred in about equal numbers. Variations in color of *P. regilla* were not observed (Test 1898). Black eye stripes were always present as reported by Brattstrom and Warren (1955).

Periodically, from February to July 1986-1989, 10 light green *P. regilla* were kept in a brown aquarium, and within 1 h all individuals changed to a dark green phase. Even after 120 h no green frogs turned brown. Most dark green frogs turned a lighter green in an open aquarium. Captive chorus frogs were not kept after 5 days because they did not feed. These observations supported those of Brattstrom and Warren (1955) and Resnick and Jameson (1963), who reported that the primary green coloration and black eye stripes are genetically determined, while the color phases and

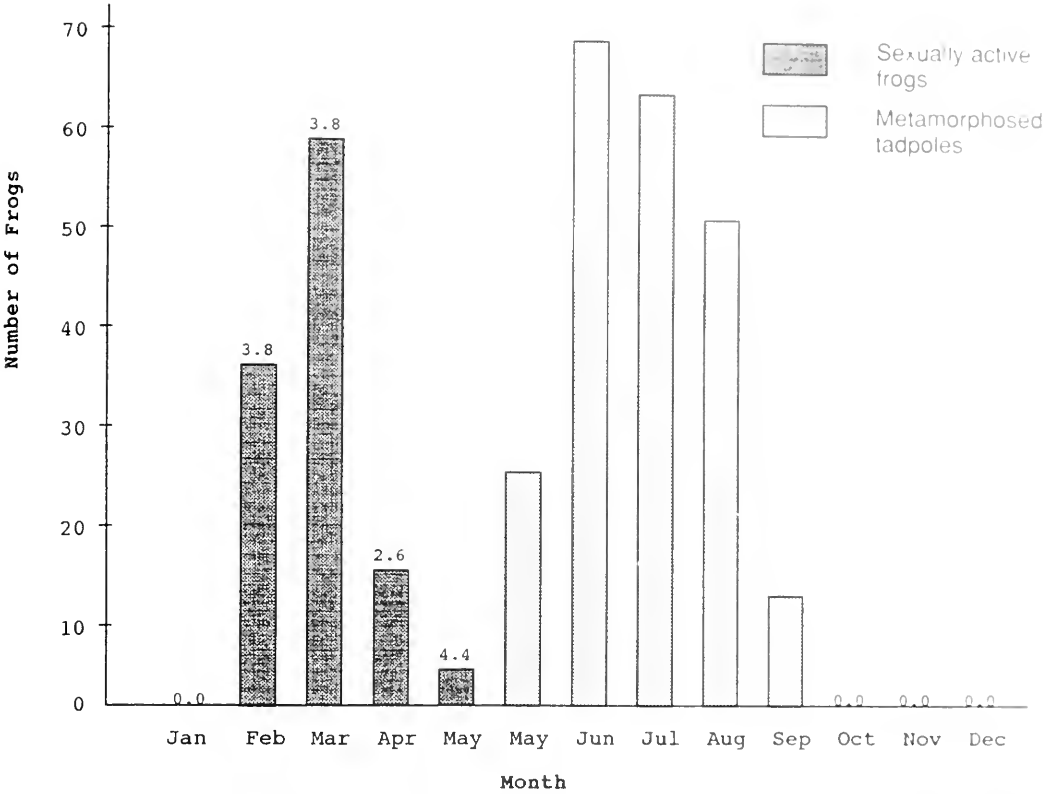

Fig. 1. Average number of frogs during each month for 12 of the 15 years (1974–1989). Counts were made at night. Top numbers are the standard deviations.

spots are environmentally regulated. Season, locality, and, to some extent, age also affect color (Resnick and Jameson 1963). Neither albinism described by Resnick and Jameson (1963) nor limb abnormalities reported by Reynolds and Stephens (1984) were observed in these populations of *P. regilla* during the 15 years of observation.

Natural Physical Disturbances

From 1905 to 1989 the chorus frog population in the breeding pond was annihilated 10 times. From 1975 to 1989, in 1975, 1983, and 1986, the time of this study, the chorus frog population in the pond was eliminated three times by flash floods. For 12 of these 15 years (80%), chorus frogs produced offspring that completed metamorphosis. Heavy rainfalls, along with melting snow at higher elevations, or prolonged downpours caused Bailey Creek to become a rushing torrent, rising up to 1 m above normal pond level. Twice during the study violent thunderstorms were observed, and they generated rapidly moving mudflows that scoured the streambed. In addition to flash flooding, sudden drastic rises in pond water temperature and drought conditions also reduced the chorus frog population in the pond. In six of the years, from 1974 to 1989, in March and April, the pond water temperature rose from 7 C to 21 C within 20 days. This sudden rise in pond water temperature had a negative impact on the chorus frog population for those years. In three of the years a light snowpack and sparse rainfall created drought conditions; both Bailey Creek and the pond dried up.

Predation

During the study three predatory species, the belted kingfisher (*Megaceryle alcyon*), western terrestrial garter snake (*Thamnophis elegans*), and domestic cat (*Felis domestica*), were observed taking chorus frogs.

The belted kingfisher preyed on both larvae and adults in the water. Throughout the

TABLE 1. Number of adult frogs during the study period, February–May 1975–1989.

Year	February	March	April	May
1975[a]	1	0	0	0
1976	36	55	19	11
1977	38	64	15	8
1978	37	61	17	2
1979	39	62	14	9
1980	31	53	10	12
1981	39	58	13	16
1982	35	56	15	5
1983[a]	1	4	0	0
1984	39	57	13	3
1985	45	60	16	8
1986[a]	2	0	0	0
1987	34	64	19	0
1988	31	66	17	8
1989	41	63	17	10
Mean ± SD	37 ± 3.8	60 ± 3.8	15 ± 2.6	8 ± 4.4

[a] Not used to determine mean and standard deviation.

study, except for those years when the chorus frog population was destroyed by flash flooding, observations were made of kingfishers preying on chorus frogs. Frequently two kingfishers, sometimes three, took prey between 0600 and 0830 PST from February to July. A kingfisher typically dove into the water from a willow branch over the pond, returned to a perch with a tadpole, and then swallowed the entire organism. After catching a frog, the kingfisher flew to a perch, bashed the frog against the limb on the left and right sides alternately, and then swallowed the dead frog.

On 20 occasions from 1974 to 1989 western terrestrial garter snakes were observed within 4 m of or in the pond. Often three to five snakes were counted at one time. Mrs. George Minor (personal communication) remembered western terrestrial garter snakes being very numerous in the canyon, especially near the pond. On 10 different occasions she remembered seeing snakes take chorus frogs while on the bank or near shore. Brattstrom and Warren (1955) and Jameson (1956) listed garter snakes as predators of *P. regilla*.

At various times during the study at least 20 domestic house cats were abandoned near the study site. On four occasions cats were observed capturing frogs while on the bank. After each instance one to three bitten, battered, and torn frogs were found. These frogs were never eaten; they were victims of the hunting, playing, and killing behavior characteristic of house cats.

DISCUSSION

Riparian habitats such as Bailey Creek in the desert of northwestern Nevada are rare. The nearest water site to Bailey Creek is an irrigation ditch 5000 m west. The study pond area associated with Bailey Creek is the only breeding site for *P. regilla* along this creek. This indicates the significant role that breeding sites play in determining the distribution and survival of the chorus frog and other amphibian species. Jameson (1956) also concluded that the distribution of breeding sites was a limiting factor for chorus frogs.

In addition to breeding sites, cool, moist microhabitats are significant for the survival and distribution of chorus frogs. Pacific chorus frogs have been found in several of these habitats in northwestern Nevada. Eight chorus frogs were observed under plywood located on a mudflat, 10 were noted inside an isolated concrete, boxlike structure that was once used to store water at a spring (several meters from other places of free water), and 2 were noted in a housing unit for valves that operated a sprinkler system.

At precise times of the year chorus frogs migrate to and from these isolated microhabitats. In the early spring of the year during the breeding season, migration is toward the breeding pond. After metamorphosis is completed at the breeding ponds, migration is away from the pond toward a cool, moist microhabitat. During this study the chorus frog population at the study site was annihilated

TABLE 2. Average daytime ambient and pond water temperatures. Ambient temperatures were recorded 1 m above the ground and 3 m north of the pond. Pond water temperatures were recorded at 15 cm at the center of the pond.

Month	Ambient $\bar{x}$ daytime temperature (°C)	$\bar{x}$ pond water temperature (°C)
January	4	4
February	7	7
March	11	12
April	13	12
May	16	12
June	19	16
July	23	16
August	24	19
September	19	12
October	19	11
November	11	5
December	3	2

TABLE 3. Frog activity associated with time of year and range of both ambient and water temperatures.

Frog activity	Time of year	Temperature range (°C)	
		Water	Air
Entered pond, chorusing, and mating	Late February–early April	7–11	[illegible]
Oviposition	Mid-march–mid-May	[illegible]–12	11–16
Hatching and tadpole development	Mid-April–early August	11–18	12–22
Exit of sexually active adults	Late April–early May	12	14
Completion of metamorphosis	Late May–late September	12–16	16–18
Exit of metamorphosed tadpoles	Late August–early October	10–18	20–24
Very few or no frogs in the pond	Early October–late February	7–10	[illegible]–20

three times. Yet, each time during the next year's breeding season (1976, 1984, and 1987) chorus frogs were present in numbers similar to those of other years at the study site. The likely explanation is that chorus frogs living in microhabitats in the vicinity of the study site migrated to the breeding pond the year after the population was annihilated.

In late February adult males located and entered the pond probably in response to a rise in ground, water, and air temperatures (Table 2). Brattstrom and Warren (1955) concluded that at 10° C frogs will go to the water to breed. It is significant to note that *P. regilla* preferred lower temperatures than other hylids. This preference for lower temperatures was demonstrated at this site in that the temperature at which the frogs go to the pond to breed (Table 3) is on the average 5° C colder than that reported by Brattstrom and Warren (1955). In this study no warm rains occurred in February to initiate the movement of males to the pond; however, Jameson (1956) believed the first warm rains and a rise of reproductive hormones cause adult males to move to breeding ponds.

This study indicates that males remain in the pond during the entire but short breeding season. Jameson (1957) suggested that males migrate to the pond, breed, exit, and are replaced by other males. Attempts by males to establish and defend territories, i.e., trill calls, butts, and wrestling bouts (Perrill 1984) and territorial compression as other frogs enter the pond (Whitney and Krebs 1975), were not observed.

Throughout the study the isolated population of the Pacific chorus frog was subjected to a variety of environmental resistance. Yet it was never eliminated; clearly, it is well adapted to a habitat that is subjected to periodic natural physical disturbances such as heavy rains, flash floods, and droughts.

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ASSOCIATION OF BLACK-TAILED PRAIRIE DOG COLONIES WITH CATTLE POINT ATTRACTANTS IN THE NORTHERN GREAT PLAINS

Daniel S. Licht[1,2] and K[illegible] D. S[illegible][3]

ABSTRACT.—In October 1991 we recorded all black-tailed [illegible] point attractants in a 1248-km² study area in southwest North Dakota [illegible] were defined as fabricated water tanks and long-term supplemental [illegible] prairie dog colonies encompassed or adjoined cattle point attractants (< [illegible] cattle point attractants were a mean distance of 1.0 km from [illegible] tants may encourage prairie dog colonization. Conversely, [illegible] discourage prairie dog colonization.

Key words: prairie dogs, cattle, dispersal, management, [illegible]

Forage relationships between black-tailed prairie dogs (*Cynomys ludovicianus*) and cattle have been described in the literature (Hansen and Gold 1977, Uresk and Bjugstad 1983, Uresk 1985, Knowles 1986). However, a lesser number of authors have discussed how cattle activity can affect the creation and distribution of prairie dog colonies. Uresk et al. (1982) reported that black-tailed prairie dogs were more abundant in areas of southwest South Dakota that were heavily grazed by cattle. Koford (1958) stated that black-tailed prairie dogs inhabit areas where vegetation height was reduced by clipping plants to ground level.

Conversely, other authors demonstrated that increased vegetation height inhibits increases in prairie dog numbers. Snell and Hlavachick (1980) and Snell (1985) reported that prairie dogs suffered reduced expansion and elimination due to summer-deferred grazing. Cincotta et al. (1987) reported that prairie dog expansion can be inhibited by management for grasses of increased height and density.

We observed what appeared to be a disproportionate number of prairie dog colonies encompassing or adjoining cattle watering tanks and cattle supplemental feed sites. This phenomenon has been observed by other researchers (Koford 1958, Cincotta 1985, Daniel Uresk, USDA Forest Service, Rapid City, South Dakota, personal communication) but not statistically documented. The primary objective of this study was to document the correlation between the occurrence of cattle point attractants (i.e., water tanks and supplemental feed sites) and prairie dog colonies. In addition, we would analyze the spatial distribution of cattle point attractants and prairie dog colonies within the study area.

STUDY AREA AND METHODS

The 1248-km² study area (38.4 km north-south by 32.0 km east-west) is in Bowman and Slope counties in southwest North Dakota and Fallon County in southeast Montana. The southeast corner of the study area is located 4.8 km south of the town of Rhame, North Dakota (Fig. 1).

Mean annual precipitation is [illegible] and mean annual snowfall is 10[illegible]. Mean temperatures range from −11 °C in January to 21 °C in July. The mean growing season is 122 days.

The study area is [illegible] Missouri Plateau physiographic [illegible] portion within [illegible] known as the B[illegible] This area is [illegible] flat landscape [illegible] plateaus [illegible] buttes [illegible]

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ave network throughout this physiographic area. The remainder of the study area is within a Missouri Plateau subdivision known as the unglaciated area (Omodt et al. 1968). It is characterized by gently rolling topography more typical of the Great Plains.

Vegetation is typical of mixed-grass and short-grass prairies. Grasses include western wheatgrass (*Agropyron smithii*), green needlegrass (*Stipa viridula*), blue grama (*Bouteloua gracilis*), and needle-and-thread (*Stipa comata*). Grasslands comprise about 50% of the study area. A shrub/grass mixture including sagebrush (*Artemisia* sp.), western snowberry (*Symphoricarpos occidentalis*), and chokecherry (*Prunus virginiana*) constitutes about 30% of the landscape. Green ash (*Fraxinus campestris*) and Rocky Mountain juniper (*Juniperus scopulorum*) are found in woody draws and on north-facing slopes, comprising an additional 10% of the study area. The remainder of the study area consists of barren areas.

Approximately 24% of the study area occurs on public land, most of which is administered by the U.S. Forest Service. The public land is intermixed with private holdings. Cattle grazing occurs throughout the study area. Grazing systems vary from season long to deferred or rest-rotation systems. Stocking rates range from 0.9 to 1.2 ha per animal unit month.

The U.S. Forest Service controls prairie dogs on public land when prairie dog colonies expand onto private holdings or exceed their allotted acreage for primary range within the management district. Primary range is defined by the U.S. Forest Service as "range which livestock naturally prefer, or will use first." Most landowners zealously attempt to control prairie dogs on their land, the most common method being the use of zinc phosphide–treated grain.

On 8 October 1991 we conducted an aerial census of the study area with 3.2-km-wide transects from an altitude of 305 m. Two observers recorded all prairie dog colonies and active cattle point attractants on their respective side of the plane. Prior and subsequent field surveys indicated the aerial census recorded all but two prairie dog colonies and all cattle point attractants.

Active cattle point attractants were easily identified from the air by the network of trails leading to the point attractant and the fringe of barren ground surrounding it. Cattle point attractants were water tanks or supplemental feed sites. For purposes of this study, water tanks are defined as fabricated structures, usually made of metal, concrete, or fiberglass. Only supplemental feed sites that had evidence of a long-term pattern of use by cattle were included in the analysis.

For our study, stock dams and dugouts were not considered cattle point attractants. Because of their greater surface area, stock dams and dugouts do not concentrate cattle to the degree that water tanks and supplemental feed structures do. In addition, the soil adjacent to stock dams and dugouts is often characterized by a high water table and strong clay content. These characteristics can discourage the creation of prairie dog burrows.

Size of the prairie dog colonies was determined by field surveys using mechanical measuring wheels and topographic maps. Distances between prairie dog colonies were measured with topographic maps.

A chi-square goodness-of-fit analysis was conducted on the number of cattle point attractants observed in or adjoining prairie dog colonies versus the number expected. A Mann-Whitney (Mann and Whitney 1947) test was used to compare the size of prairie dog colonies with associated cattle point attractants versus colonies without associated cattle point attractants.

Results

Fifty-one prairie dog colonies were identified within the study area, ranging in size from 0.1 to 112.0 ha ($\bar{X}$ = 15.4 ha). Total prairie dog acreage on the study area was 784.5 ha, or approximately 0.6% of the study area. Prairie dog colonies were distributed throughout the study area with the exception of the extreme northwest corner (Fig. 1).

One hundred four active cattle point attractants were identified in the study area. A density of 1 cattle point attractant per 12.0 km^2 was observed in the 1248-km^2 study area. Fourteen cattle point attractants were within or adjoining prairie dog colonies.

A chi-square goodness-of-fit test of the number of cattle point attractants in or adjoining prairie dog towns (n = 14) versus the number expected (prairie dog acreage / study

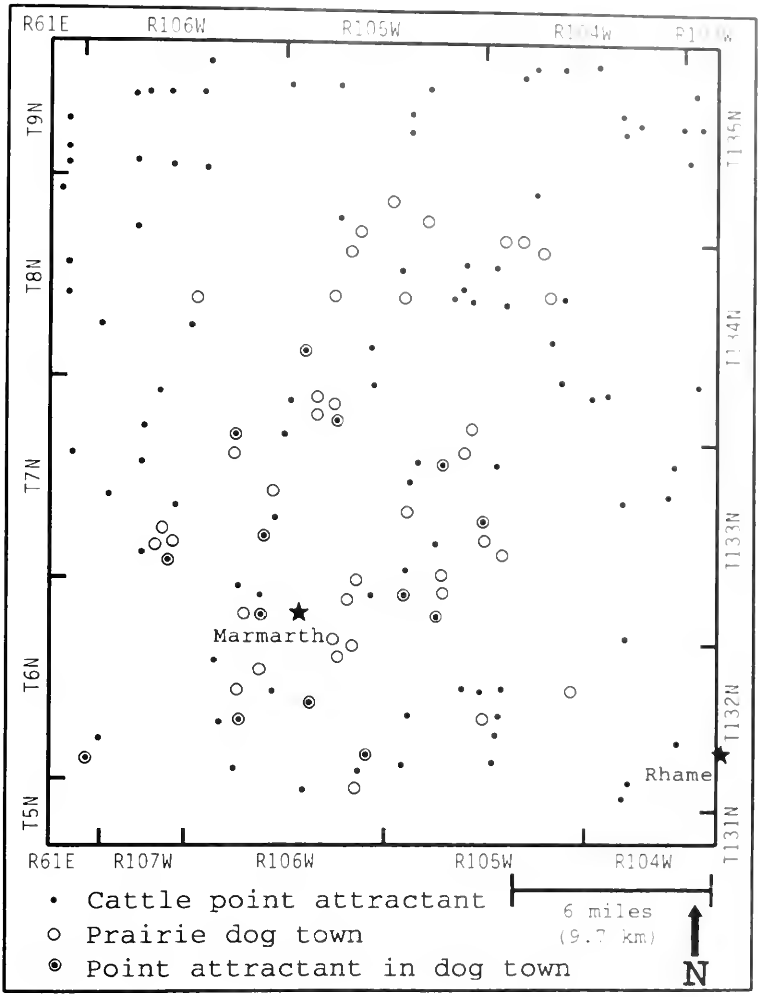

Fig. 1. Distribution of cattle point attractants and prairie dog colonies in the study area. Symbols do not represent the actual scale of the cattle point attractants or the prairie dog colonies.

area acreage × number of point attractants = 0.65) revealed that prairie dog colonies were significantly more likely to be associated with cattle point attractants than expected ($X^2 = 272.4$, 1 df, $p < .001$). When only prairie dog colonies <5 ha were analyzed, the number of cattle point attractants in or adjoining prairie dog colonies ($n = 7$) versus the number expected ($n = .04$) had a higher X^2 value ($X^2 = 1181.6$, 1 df, $p < .001$). A Mann-Whitney test revealed no statistically significant difference in size between prairie dog colonies with associated cattle point attractants versus colonies without ($U = 270.0$, $n_{37,14}$, $p = .184$).

The mean distance of prairie dog colonies with associated cattle point attractants to the next nearest prairie dog town was 1.0 km ($n = 13$, range = .1–2.6 km). One town was excluded from analysis because it was on the perimeter of the study area. Prairie dogs that originally established the town may have come from unknown colonies outside the study area.

DISCUSSION

Prairie dog dispersal is an evolutionary adaptation with a variety of purposes, including colonization of new areas. Garrett (1982) tracked one dispersing prairie dog 7 km before it settled at the edge of an existing prairie dog town.

[illegible] cattle point attrac- tants [illegible] may [illegible] lessening the [illegible] However, we found [illegible] The actual [illegible] may be greater than [illegible] prairie dogs [illegible] have [illegible] all [illegible]

Our data showed a significant correlation between the presence of cattle point attractants and the occurrence of [illegible] prairie dog colonies. We cannot prove that cattle point attractants were established first and thus caused the [illegible] by prairie dogs. However, based on field observations and a review of the literature, we feel strongly that this was the case in most instances.

Cattle point attractants are characterized by grazed and trampled vegetation and therefore high visibility for prairie dogs. Cincotta (1985) reported that dispersing prairie dogs [illegible] areas [illegible] existing prairie dog colonies that had low vegetation and therefore high visibility for prairie dogs. Koford (1958) reported that a small prairie dog town [illegible] than [illegible] bare ground that surrounded a [illegible] tree. The tree was a [illegible] Our [illegible] consistent with [illegible] prairie dogs [illegible] areas with high visibility. We [illegible] significant correlation [illegible] the presence of cattle point attractants [illegible]

[illegible]

vegetation and high visibility are conducive to prairie dog colonization (Koford 1958, Uresk et al. 1982, Cincotta 1985). We believe that cattle point attractants can create a microenvironment with these characteristics and facilitate prairie dog expansion. The creation of cattle point attractants in close proximity to prairie dog colonies (0.1–2.6 km) may promote the establishment of new colonies. Conversely, we believe that the establishment of new prairie dog colonies can be suppressed by refraining from using cattle point attractants. Moving cattle point attractants before a condition of low vegetation develops may also discourage prairie dog expansion.

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HUMAN FATALITIES CAUSED BY VENOMOUS ANIMALS IN UTAH, 1900–90

Richard C. Straight[1] and James L. Glenn[1]

ABSTRACT.—An examination of death certificates at the Utah Bureau of Health Statistics from 1900 through 1990 indicates that Utah has a very low incidence of human fatalities due to venomous bites and stings. During this 91-year period, 20 fatalities were recorded from bee (10) or hornet (1) stings, spider bites (4), and rattlesnake bites (5). There were eight additional fatalities during the early part of this century recorded from "insect bite," "apparently insect bite," or "unknown agent poisoning," some of which may have included spiders. No deaths were recorded from Gila monster or scorpion envenomizations, although in 1962 one death in San Juan County was recorded as "venom poisoning, unknown agent, possible scorpion." Utah statistics follow the national pattern, indicating that bee stings cause more fatalities than spider bites or rattlesnake bites. Rapid deaths (within minutes) occurred in the majority of bee sting fatalities, resulting from allergic reactions (anaphylaxis), whereas protracted death times of days or months, resulting from infection, followed most spider and unknown insect bites. Only two spider bite fatalities occurred within 1–3 days, suggesting black widow envenomization. Two of the five fatalities from rattlesnake bite resulted from handling the offending snake, one fatality was recorded as a homicide, and one other envenomization occurred in Arizona, with subsequent death in Utah.

Key words: fatalities, envenomization, venomous animals, rattlesnakes, spiders, hymenopterids, scorpions, Gila monsters, tick bite, Utah.

Venomous animals native to Utah and considered dangerous to humans include hymenopterid insects (bees, hornets, wasps), spiders, scorpions, and reptiles (rattlesnakes and Gila monster). Three species of mildly venomous snakes (Colubridae) are considered to be medically unimportant. The only national study of the incidence of fatalities from all venomous animal bites or stings is the 1950–59 survey by Parrish (1963). He obtained his data through the National Office of Vital Statistics and subsequently reviewed death certificates from each state in which deaths occurred. His survey indicated that Hymenoptera stings cause more human fatalities than all other venomous animals combined. Only one fatality from Hymenoptera sting occurred in Utah during this 10-year period, and no Utah fatalities from rattlesnake bite were recorded (also see Parrish 1966, 1980). In the present investigation we examined death certificate records at the Utah Bureau of Health Statistics for fatalities recorded as caused by all venomous animals from 1900 through 1990. The results of the 91-year survey are presented in this report.

METHODS

Death certificates were surveyed at the Utah Bureau of Health Statistics for the cause of death due to animal bites and stings. Therefore, even deaths from diseases transmitted by tick bite were gathered and are briefly discussed in this report. At the time of this survey, death certificates prior to 1956 were not coded as to cause of death, necessitating that every certificate be examined. Death certificates filed since 1956 are coded as to cause of death by the International Cause of Death Code (ICD) and were screened using these codes.

RESULTS

Fatalities from Hymenopterid Stings

Eleven fatalities from hymenopterid stings were recorded in Utah during the 91-year period 1900–90 (Table 1). The first recorded fatality during this period was in 1904 (from infection) and the most recent in 1984, the latter being the only year with more than one fatality. The majority were recorded as "bee"

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sting. One fatality was ascribed to a "hornet" sting (1922), and one was the result of multiple bee stings while the victim was gathering firewood at the Strawberry Reservoir area (1980). One victim (1984) was stung in Nevada but died in Utah 36 h later. Most deaths occurred rapidly by anaphylaxis, but two deaths (1984) were due to cardiovascular or myocardial injury induced by the anaphylactic reaction. The delayed death times of the latter victims likely reflect patients kept alive with various modern medical techniques. Deaths occurred in the summer months, the majority in July and August. All age groups (7–71) are represented. Notably, after the 1954 fatality, 26 years passed without a bee sting fatality and then four deaths occurred in the 5-year period 1980–84 (Table 1). The 1980s was the only decade to contain four fatalities from hymenopterid sting.

Spider Bite Fatalities

Only four deaths were recorded from "spider bite," and two of these were recorded as "probable" spider bites (Table 2). Three of these four cases were children less than 6 years of age, with deaths resulting in 3–25 days from "blood poisoning," "infection," or "septicemia" (before antibiotics, 1915–36). One death (1968), listed as "acute circulatory failure—probable poisonous spider bite on leg," occurred in 21 h to a 41-year-old "mentally retarded" male (American Fork, Utah). Eight additional fatalities recorded in the earlier part of this century were caused by chronic infection from "insect bite" or "unknown agent" poisonings. These may have been from spider bite but are not included herein. The time of death in these cases was quite delayed, about 2–5 months. The "suspected" spider bite deaths and other "insect" bite deaths occurred in all seasons of the year.

Scorpion Sting Fatalities

The only Utah fatality recorded as "venom poisoning, unknown agent, possibly scorpion" was a 24-year-old female Indian at Monument Valley Hospital, San Juan County, on 31 December 1962. The death certificate does not mention infection, but rather "venom poisoning," as if from the direct effects of the venom. The place of injury was "unknown" and the victim died in 3 days. The victim was attended by a physician for about 14 h.

Fatalities from Gila Monster Bite

The Utah distribution of the Gila monster (*Heloderma suspectum*) is limited to Washington

TABLE 1. Utah fatalities recorded as caused by Hymenoptera stings during the period 1900–90

Date	Sex	Age	Death	Comments
9/17/1904	F	71 yr	18 d	"Blood poisoning"
7/08/1922	M	39 yr	5–10 min	"Hornet" sting
8/17/1926	F	15 yr	30 min	"No doctor available"
7/28/1929	M	12 yr	2 d	"Was sensitized to bee sting"
8/13/1935	F	28 yr	30 min	"Idiosyncrasy to bee sting"
8/06/1936	M	46 yr	10 min	"Stung above right eye—riding horse"
7/11/1954	F	53 yr	30 min	"Anaphylactic shock, bee sting"
9/13/1980	M	43 yr	minutes	"Anaphylaxis, bee stings"
8/08/1983	M	7 yr	2 d	"Anoxic encephalopathy"
6/26/1984	M	60 yr	36 h	"MI, rupture myocardium"
9/17/1984	F	63 yr	5 d	Victim stung in Nevada

TABLE 2. Human fatalities in Utah recorded as caused by spider bite during the period 1900–90[a]

Date	Sex	Age	Death	Comments
12/18/1915	F	4 1/2 mo	25 d	"Septicemia, spider bite"
10/03/1923	F	5 1/2 yr	3 d	"Blood poisoning, probably spider"
8/04/1926	M	15 mo	7 d	"Abscess of face caused by spider"
3/27/1968	M	41 yr	21 h	"Acute circulatory failure, probably spider bite"

[a] There are eight additional fatalities during the early part of this century recorded from chronic infections (apparently insect bite or unknown agent poisoning), some of which may have included spiders. Death times were 2–5 months from infection.

Table 3. Human fatalities in Utah recorded as caused by rattlesnake bite during the period 1900–90[a].

Date	Sex	Age	Death	Comments
7/17/1931	M	12 1/2 yr	1 d	"Poisoning from rattlesnake venom"
6/19/1938	M	22 yr	4 h	"Rattlesnake bite, possible intracranial hemorrhage with hysteria"
8/22/1961	F	70 yr	24 h	"Rattlesnake bite in outdoor Hogan"
10/04/1963	F	10 yr	11 1/2 h	"Rattlesnake bite, Mexican Water, AZ"
5/07/1987	F	22 mo	5 h	"Venomous bite, snake held by another person" (resulting in homicide)

[a] Not included are a 1913 fetal death (miscarriage) and an exotic snakebite fatality in 1964. See text.

County in the extreme southwestern region of the state. No fatalities from envenomization by the Gila monster were reported in Utah during the 91-year period, according to our survey.

Rattlesnake Bite Fatalities

Extenuating and/or unusual circumstances were associated with three of the five rattlesnake bite fatalities in Utah (Table 3). In 1931 the death of a 12-year-old boy was recorded as "poisoning from rattlesnake venom"; however, the exact cause was questionable. The child had reportedly handled a dead rattlesnake (*Crotalus viridis lutosus*) "a day before he became ill" (*Beaver News*, page 1, 24 June 1931). Apparently, however, the child was not attended by a physician and no autopsy was performed. A second unusual death (19 June 1938) was attributed to "possible intracranial hemorrhage with hysteria," resulting from head injuries incurred during the victim's hysteria following envenomization by a rattlesnake (*C. v. lutosus*). The hiking victim was attempting to kill ("cut in half") the rattlesnake in South Willow Canyon, near Grantsville (*Salt Lake Tribune*, page A-20, 20 June 1938). As the victim was being transported by car down the canyon, he "flung himself around in apparent hysteria, striking his head several times on the back of the rear seat." This 22-year-old male died in approximately 4 h en route to Salt Lake City. A third unusual death was a tragic fatality (1987), recorded as a homicide, which resulted when a large rattlesnake (*C. v. lutosus*) bit a 22-month-old girl after the snake had been placed around her neck (Washington County). The child died in approximately 5 h.

In 1961 a 70-year-old female was bitten by *Crotalus v. viridis* and died within 24 h (Monument Valley, San Juan County). This is the only Utah fatality in which rattlesnake envenomization occurred within the state borders and the victim did not handle the snake. One 10-year-old girl was bitten (*C. v. viridis*) in northeastern Arizona but was hospitalized and died in Utah (San Juan County, 1963) 11 1/2 h after envenomization.

Two additional human fatalities in Utah have involved snakes. In 1913 a fetal death (aborted stillbirth—5 months) was ascribed to "shock" caused by the mother "almost stepping on a snake" (Cedar City). Also, Utah has one recorded fatality (1964) that was caused by the bite of a captive exotic snake (African puff adder, *Bitis arietans*). The 37-year-old male, director of Hogle Zoological Gardens, Salt Lake City, died in 31 h. This incident is one of only two venomous snake–induced fatalities this century in American zoological institutions.

Fatalities Resulting from Tick Bite Diseases

Although tick bites may not be considered envenomizations per se, it is appropriate to include them in this review of deaths resulting from bites and stings of dangerous animals. Two different febrile diseases can be transmitted by tick bite in Utah and other Rocky Mountain states, i.e., Colorado tick fever and Rocky Mountain spotted fever (see Dyer 1963, Eklund 1963). Forty-six fatalities were attributed to tick bite and recorded as "tick fever" (7), "spotted fever" (15), or "Rocky Mountain spotted fever" (24). All but one of the deaths occurred during the period 1900–42 (Table 4). The victims were typically middle-aged male farmers or sheepmen in mountainous terrain. Most victims were bitten from early spring through midsummer. Consequently, before the advent of antibiotics, fatalities from disease-bearing ticks greatly outnumbered all venomous animal–induced fatalities in Utah. However, venomous

TABLE 4. Human fatalities recorded as due to Rocky Mountain spotted fever or tick bite from 1900–90.

Years	1900–09	1910–19	1920–29	1930–38	1942	1955[a]
Deaths	8	15	10	12	1	1

[a] Death resulting from "gas gangrene."

animal–induced fatalities, mainly rapid death by anaphylaxis from Hymenoptera sting, now overshadow tick bite fatalities, as the last tick bite fatality (from "gas gangrene") occurred in 1955.

DISCUSSION

Spider bites often occur while the person is asleep and may produce little or no immediate pain, symptoms are slow to develop, and the offending spider is seldom seen or identified. Conversely, bee or hornet stings cause immediate pain and the envenomer is usually seen by the victim. Also, the vast majority of deaths from spider or "insect" bite are protracted over days (from infection), whereas bee sting causes rapid death within minutes from anaphylaxis or within a matter of hours due to cardiovascular injury induced by the anaphylactic reaction. Only one death (1968) from "probable spider bite" has occurred in Utah since the discovery and widespread use of antibiotics. This case is suspected to be the result of black widow (*Laterodectus*) envenomization. Although the black widow is relatively common around human habitations throughout Utah and is capable of causing death (rare) to humans, no fatalities in which this spider was specifically identified have been recorded in Utah.

Only one species of scorpion in the USA is considered capable of killing humans with a single sting, i.e., *Exilicauda sculpturatus* (formerly *Centruroides* genus). This species is abundant in the deserts of Arizona and has been collected in southeastern Utah at Hole-in-the-Rock (Kane County, Utah) in 1953 (Johnson and Allred 1972). There have been a few scorpion stings in the southeastern region of Utah resulting in severe pain and neurological signs similar to *E. sculpturatus* stings (personal communication with personnel at Moab Hospital and Canyonlands National Park). The distribution of this scorpion in Utah is presently unknown but is likely limited to the Colorado River drainage areas in the southeastern region of the state.

Snakebite envenomizations are often divided into two categories, legitimate and illegitimate. Envenomizations in which the victim is unaware of the offending snake are considered legitimate; e.g., the victim accidentally steps, sits, or places hand on or near the snake in the wild (or yard). Illegitimate snakebites include envenomizations by captive specimens or by specimens whom the victim attempts to handle, kill, or manipulate. Only two of the snakebite fatality victims discussed above would be classified as legitimate category envenomizations (1961, 1963) but one of these was not bitten in Utah (Arizona—1963). One death involved homicide (1987). Two involved psychological effects of fear or hysteria (1913, 1938), and one of these may even have involved a harmless snake (1913). One death involved an exotic species in captivity (1964), and one mysterious death possibly involved handling a dead rattlesnake (1931). According to state localities of the snakebites in Utah, only two subspecies of rattlesnakes (*C. v. viridis* and *C. v. lutosus*) have been involved. No deaths have been recorded from areas of *C. v. concolor* distribution in eastern Utah, and no fatalities are indicated from *C. cerastes*, *C. scutulatus*, or *C. mitchelli*, which are limited to Washington County in southwestern Utah. Only three Utah fatalities from envenomizations by the Great Basin rattlesnake (*C. v. lutosus*) occurred during the 91-year period, and all three involved handling of the snake (illegitimate envenomization category).

Utah has a very low incidence of human fatalities from venomous bites and stings. Hymenoptera are responsible for more human deaths than all other venomous animals combined, which follows the national statistical pattern (Parrish 1963). Fatalities due to rattlesnake envenomization represent an extremely low environmental hazard and would be further reduced if rattlesnakes were not handled. Hymenopterid sting fatalities could be reduced if emergency self-treatment kits (epinephrine in dose syringes) were carried by persons suspected of allergy to bee venom.

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SOME NEW RECORDS OF NAIDIDAE AND TUBIFICIDAE (ANNELIDA: OLIGOCHAETA) FROM WASHINGTON

Douglas R. Spencer[1] and Robert L. Wisseman[2]

ABSTRACT.—Five species of Naididae (*Ophidonais serpentina*, *Uncinais uncinata*, [illegible], *Dero digitata*, and *Slavina appendiculata*) and six species of Tubificidae (*Tasserkidrilus harmani*, [illegible], *A. pluriseta*, *A. pigueti*, *A. americanus*, and *Branchiura sowerbyi*) are reported for the first time from Washington. *T. harmani*, *A. pigueti*, and *A. americanus* are also new to the fauna of the western United States. Descriptions and distribution ranges are provided for the new records. A checklist of the freshwater species occurring in Washington is provided.

Key words: Annelida, Oligochaeta, Naididae, Tubificidae, Nearctic distribution, Washington, [illegible] *zoogeography.*

Altman (1936) initially described the oligochaete fauna of Washington. Several families of Oligochaeta were listed in his report including the documentation and description of a number of species within the Lumbriculidae, Haplotaxidae, Naididae, and Tubificidae. Many of those records were reviewed and verified by Brinkhurst (1964, 1965) and Brinkhurst and Cook (1966), and additional species were added to the Washington list by Thut (1969) and Smith (1984). Recently, Brinkhurst and Kathman (1983) published several new distributional records for Washington state, and Brinkhurst (1981) described a new species of Tubificidae from Mowich Lake in Mount Rainier National Park.

During the identification of several collections of freshwater oligochaetes, the senior author identified 32 species within the families Naididae and Tubificidae from four lake systems in the Seattle area. Of these, 11 species were discovered that had not been reported previously from the state of Washington. Three species were also found to be new to the Western United States.

METHODS AND MATERIALS

Oligochaetes for this paper were identified from benthos collections taken during environmental studies for the Municipality of Metropolitan Seattle and the Washington State Department of Ecology. Specimens were obtained from Black Lake (Thurston County), Lake Steilacoom (Pierce County), and Lakes Union and Washington (King County).

Samples were initially fixed in formalin and specimens preserved in 70% alcohol. Worms were prepared for identification by mounting them on microscope slides in Ammans Lactophenol as described by Brinkhurst (1986). The oligochaetes were then identified under the microscope at 100X or greater magnification.

AQUATIC OLIGOCHAETA NEW TO WASHINGTON

NAIDIDAE

Ophidonais serpentina (Muller 1773)

LOCALITY.—PIERCE CO.: Lake Steilacoom, 26 November 1990. THURSTON CO.: Black Lake, 27 November 1990.

DESCRIPTION.—Body ca 6 mm long, width anteriorly 0.37 mm and 0.53 mm posteriorly. Body consisting of ca 62 segments. Prostomium triangular, rounded at apex, without proboscis. Eyes present. Body with pigmented stripes on anterior segments; cuticle appears somewhat granular in some specimens. Anteriorly, dorsal chaetae present from segment VI (although missing from some segments), each fascicle containing 1 straight stout chaetae ca 150 µm long with [illegible]

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ca. 1/4 from the distal end) slightly notched at apex. Ventrally, 2–4 bifurcate chaetae, 130–174 µm long, with distal and proximal teeth equal in length, proximal thicker. Posteriorly, dorsal aciculars identical to those more anterior (107–116 µm long) with 1 per fascicle. Ventrally, 3–4 bifurcate chaetae per fascicle, 100–130 µm long, identical to those more anterior. No sexually mature specimens were collected.

Distribution.—Brinkhurst (1986) reported *O. serpentina* as being widespread in North America. The species appears to be distributed from the northeastern states to Kentucky and the Ohio–Upper Mississippi River area and the Great Lakes region, and westward.

Uncinais uncinata (Ørsted, 1842)

Locality.—King Co.: Lake Union, 22 April 1991.

Description.—Body ca. 5.8 mm long, width anteriorly 0.26 mm and 0.25 mm posteriorly. Body consisting of ca. 47 segments. Prostomium triangular with a slight elevation at apex, no proboscis. With eyes. Body without pigmentation. Anteriorly, dorsal chaetae present from segment VI, each fascicle consisting of 2–3 bifurcate aciculars, 75–87 µm long, nodulus ca. 1/2 toward distal end, teeth slightly diverging and equal in length. Ventrally, 3–4 bifurcate chaetae, 93–130 µm long, with teeth equally long or distal tooth slightly longer than proximal. Posteriorly, dorsal aciculars number 3 per fascicle, 67–87 µm long, resembling those more anterior. Ventrally, 3–4 bifurcate chaetae per fascicle, 93–102 µm long, resembling those more anterior. No sexually mature specimens were collected.

Distribution.—Brinkhurst (1986) lists the North American distribution of *U. uncinata* as being widespread. The species ranges from the northeastern states and provinces to the Great Lakes region, then to Montana and the far west, then north to include many of the southern and far northern Canadian provinces.

Arcteonais lomondi (Martin, 1907)

Locality.—King Co.: Lake Union, 22–23 April 1991; Lake Washington, 23 April 1991.

Description.—Body width anteriorly ca. 0.46–0.55 mm and 0.40–0.47 mm posteriorly. Prostomium triangular, with proboscis, 203–209 µm long. With eyes. Body without pigmentation. Dorsal chaetae present from segment VI, each fascicle consisting of aciculars and capilliform chaetae. Anteriorly, aciculars number 8–14 per fascicle, 66–77 µm long, thin and needle-shaped. Capilliforms number 3–4? per fascicle, 220–320 µm long. Ventrally, 4–7 bifurcate chaetae, 280–334 µm long, with distal tooth longer than proximal. Posteriorly, aciculars number 8–12 per fascicle, 58–73 µm long, resembling those aciculars more anterior. Capilliforms number 3–5? per fascicle, 232–290 µm long. Ventrally, 2–4 bifurcate chaetae per fascicle, 102–116 µm long, with teeth equal in length. No sexually mature individuals were collected.

Distribution.—Brinkhurst (1986) reported the species to be widespread in North America. *A. lomondi* appears to range from the northeastern states and provinces including the Great Lakes and Ohio–Upper Mississippi regions, south to Florida, then west to Lake Tahoe and Oregon, and then northward through the southern tier of Canadian provinces.

Remarks.—All specimens collected were fragmented. The number of capilliform chaetae from our specimens does not conform with published descriptions. However, the chaetae may have been broken during sample processing.

Dero (*Dero*) *digitata* (Müller, 1773)

Locality.—King Co.: Lake Union, 11 October 1990, 22–23 April 1991; Lake Washington, 23 April 1991. Pierce Co.: Lake Steilacoom, 26 November 1990. Thurston Co.: Black Lake, 27 November 1990.

Description.—Body ca. 6.8 mm long, width anteriorly 0.28 mm and 0.23 mm posteriorly. Body consisting of ca. 58 segments. Prostomium triangular, rounded at apex, without proboscis. Without eyes. Body without pigmentation. Dorsal chaetae present from segment VI, each fascicle consisting of aciculars and capilliform chaetae. Anteriorly, bifurcate aciculars number 1 per fascicle, 78–98 µm long, nodulus ca. 1/2 toward distal end, teeth of aciculars slightly diverging with distal tooth longer than proximal. Capilliforms number 1–2 per fascicle, ca. 348 µm long. Ventrally, chaetae from segment II–V, 4–5 bifurcate chaetae, ca. 160 µm long, with very long teeth, distal tooth slightly longer than proximal. Posteriorly, dorsal aciculars number 1 per fascicle, ca. 96 µm long, resembling those more anterior. Capilliforms number 1 per fascicle, ca. 320 µm long. Ventrally, from segment V posteriorad, 2–3 bifurcate chaetae per fascicle, 110–120 µm long, with much shorter teeth and length. Gills present (? 3–4 pair) on last posterior segment.

DISTRIBUTION.—Brinkhurst (1986) lists a widespread distribution for *D. digitata*. The species is found from the northeastern states and provinces south to Tennessee, then west to Kansas, Texas, and California, and then north to the southern tier of Canadian provinces.

Slavina appendiculata

(d'Udekem, 1855)

LOCALITY.—KING CO.: Lake Union, 23 April 1991.

DESCRIPTION.—Body ca. 2.0–2.5 mm long, width anteriorly 0.25–0.27 mm and 0.20–0.21 mm posteriorly. Body consisting of 29–30 segments. Prostomium rounded, without proboscis. Eyes present. Body wall papillae with possible foreign matter attached. Dorsal chaetae present from segment VI, each fascicle consisting of aciculars and capilliform chaetae. Anteriorly, aciculars number 1–2 per fascicle, 50–55 µm long, reduced to a fine, threadlike point at apex. Capilliforms number 1 per fascicle, 264–286 µm long, appearing unserrated. Capilliforms of segment VI elongated, 537–566 µm long. Ventrally, 3–4 bifurcate chaetae, 88–105 µm long, with distal teeth slightly shorter than thicker proximal. Posteriorly, dorsal aciculars number 1–2 per fascicle, 39–44 µm long, resembling those more anterior. Capilliforms number 1 per fascicle, 248–264 µm long. Ventrally, 2–3 chaetae per fascicle, 77–96 µm long, resembling those more anterior. No sexually mature individuals were collected.

DISTRIBUTION.—Brinkhurst (1986) reported *S. appendiculata* as being widespread in North America. The species has been reported from the northeastern states and provinces south to Georgia and Mississippi, then west to include the Ohio–Upper Mississippi River and the Great Lakes regions, Montana, and California, north to British Columbia and many of the far northern Canadian provinces.

TUBIFICIDAE

Tasserkidrilus harmani (Loden, 1979)

LOCALITY.—KING CO.: Lake Union, 11 October 1990.

DESCRIPTION.—Body ca. 6 mm long, 0.11 mm diameter anteriorly, 0.19 mm at segment XI, 0.18 mm posteriorly. Body with 56 segments. Prostomium triangular. Anteriorly, dorsal fascicles of chaetae consist of 1–2 pectinate, ca. 44 µm long, and 1–2 capilliform chaetae, ca. 154 µm long. Lateral teeth of pectinate chaetae with distal tooth thinner than the proximal but equal in length; 2 intermediate teeth equal in length to lateral teeth. Ventrally, anterior bundles contain 2 bifurcate chaetae, ca. 56 µm long, with distal tooth thinner and shorter than the proximal. Posteriorly, dorsal fascicles of chaetae consist of 1–2 bifurcate chaetae (1 from ca. segment XII), ca. 62–68 µm long, and 1 capilliform chaeta, ca. 264 µm long. Ventrally, 1 bifurcate chaeta, ca. 68 µm long, similar to those dorsal but larger. From segment XII, the dorsal and ventral bifurcate chaetae can be described as being sigmoid, with a very robust and thick proximal tooth, the distal tooth being shorter and thinner. Without coelomocytes.

DISTRIBUTION.—Brinkhurst (1986) indicated the distribution of the species included Louisiana, Florida, Indiana, and British Columbia, suggesting a wide distribution in North America. The present range of *T. harmani* is spotty from the Ohio Valley–Mississippi River region south to include the Gulf Coast, then west to the Pacific Northwest.

REMARKS.—Only one immature specimen was identified from the Washington material. This species is reported from the western United States here for the first time.

Aulodrilus limnobius Bretscher, 1899

LOCALITY.—KING CO.: Lake Union, 10–11 October 1990, 28 February 1991, and 22 April 1991; Lake Washington, 25 April 1991. THURSTON CO.: Black Lake, 27 November 1990.

DESCRIPTION.—Body ca. [illegible] mm long, 0.17–0.21 mm diameter anteriorly, 0.18–0.24 mm at segment XI, 0.15–0.19 mm posteriorly. Body with ca. 57 segments. Prostomium rounded. Anteriorly, dorsal fascicles of chaetae consist of 4–5 bifurcate chaetae, 25–29 µm long. From segment II–VI, bifurcate chaetae [illegible] Upper Mississippi and Great Lakes [illegible], and west to the Pacific Coast and British Columbia.

[illegible]—No sexually mature individuals [illegible] collected. All specimens were fragmented.

[illegible] Kowalewski 1914

[illegible]—[illegible] Lake Union, [illegible] February [illegible] and [illegible] April [illegible]. Lake Washington, [illegible] April [illegible] Lake [illegible] April [illegible] Black Lake, [illegible] November [illegible]

[illegible]—[illegible] segment [illegible] Actually [illegible] segment IX [illegible] laterally [illegible]

[illegible]—[illegible] North American [illegible] widespread. The species [illegible] Gulf Coast [illegible] Ohio–Upper Mississippi [illegible] Great Lakes [illegible] west to the Pacific Coast [illegible] northern Cana[illegible]

[illegible]—This species is [illegible] the western United States here for the first time.

[illegible] Brinkhurst and [illegible] Cook

[illegible]—[illegible] Lake Union, [illegible] April [illegible]. Lake Washington, [illegible] April [illegible]

[illegible]—[illegible] anteriorly, [illegible] segment VII [illegible] posteriorly [illegible] rounded to triangular [illegible] ment II–VI or VII [illegible] consist of 5–10 [illegible] pectinate chaetae [illegible] tal tooth much shorter [illegible] mal, most chaetae [illegible] between lateral teeth. [illegible] VII, apex of dorsal chaetae [illegible] at 1000X [illegible] of chaetae contain [illegible] long, similar in shape [illegible] similar morphological [illegible] or VII. Posteriorly [illegible] contain 3–9 chaetae [illegible] identical to those [illegible] Ventrally, 3–9 chaetae [illegible] similar to those [illegible] ment VI or VII. With [illegible]

DISTRIBUTION.—[illegible] the North American [illegible] carus to be the eastern [illegible] Great Lakes [illegible] Saskatchewan, and [illegible] ranges from the [illegible] provinces through the [illegible] Mississippi and Great Lakes [illegible] west to the Pacific Northwest [illegible] the lower tier and far [illegible] provinces.

REMARKS.—The [illegible] were fragmented. No [illegible] uals were found. A [illegible] here for the first time [illegible] ed States.

Branchiura sowerbyi Beddard, 1892

LOCALITY.—Kin[illegible] Lake [illegible] October 199[illegible], 22 April 199[illegible] ton, 23 April 1991 [illegible] coom, 26 November 19[illegible]

DESCRIPTION.—B[illegible] mm diameter anterior [illegible] ment XI, (3[illegible] ca. 85 segments. Prostomium [illegible] riorly, dorsal fascicles [illegible] bifurcate, 103–165 µm [illegible] form chaetae, 243–33[illegible] of bifurcate chaetae [illegible] capilliform chaetae [illegible] Ventrally, 3–1[illegible] sigmoid [illegible] 81–209 µm long [illegible] V or VII. Posteriorly, dorsal fascicles consist of 2–5 bifurcate, 82–1[illegible]

[illegible] freshwater microdrile [illegible] Haplotaxidae, Naididae, [illegible]

Taxa
LUMBRICULIDAE
Kincaidiana hexatheca Altman, 1936
Rhynchelmis elrodi Smith and Dickey, 1918
[illegible] Altman, 1936
[illegible] Smith, 1895
*[illegible] McKey-Fender, 1988
HAPLOTAXIDAE
Haplotaxis gordioides Hartmann, 1821
NAIDIDAE
Chaetogaster diastrophus Gruithusen, 1828
C. diaphanus Gruithuisen, 1828
C. limnaei von Baer, 1827
Amphichaeta leydigi Tauber, 1879
Ophidonais serpentina Müller, 1773
Uncinais uncinata Orsted, 1842
Specaria josinae Vejdovsky, 1883
Pristina leidyi Smith, 1896
P. aequiseta Bourne, 1891
Stylaria lacustris Linnaeus, 1767
Arcteonais lomondi Martin, 1907
Dero (Dero) digitata Müller, 1773
D. (D.) obtusa d'Udekem, 1855
Slavina appendiculata d'Udekem, 1855
Vejdovskyella comata Vejdovsky, 1883
Nais behningi Michaelsen, 1923
N. pseudobtusa Piguet, 1906
N. communis Piguet, 1906
N. variabilis Piguet, 1906
Pristinella jenkinae Stephenson, 1931
TUBIFICIDAE
Tubifex tubifex Müller, 1774
Tasserkidrilus harmani Loden, 1979
Limnodrilus hoffmeisteri Claparède, 1862
L. claparedianus Ratzel, 1868
Ilyodrilus templetoni Southern, 1909
I. frantzi Brinkhurst, 1965
Varichaetadrilus pacificus Brinkhurst, 1981
Spirosperma nikolskyi Lastockin and Sokolskaya, 1953
Quistadrilus multisetosus Smith, 1900
Aulodrilus limnobius Bretscher, 1899
A. pluriseta Piguet, 1907
A. pigueti Kowalewski, 1914
A. americanus Brinkhurst and Cook, 1966
Rhyacodrilus montana Brinkhurst, 1965
Bothrioneurum vejdovskyanum Stolc, 1886
Branchiura sowerbyi Beddard, 1892

[illegible]

streams of the Cascade Range, and many of the water bodies east of the Cascades.

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[illegible]

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DISTRIBUTION OF THE SOUTHWESTERN TOAD (*BUFO MICROSCAPHUS*) IN ARIZONA

Brian K. Sullivan[1]

Key words. Bufo microscaphus, *southwestern toad, Arizona, distribution, amphibian decline, riparian habitat, hybridization.*

The current distribution and status of populations of the southwestern toad, *Bufo microscaphus*, are of considerable interest given the suspected decline in anuran amphibians in the western United States (Blaustein and Wake 1990, Sweet 1991). This bufonid, typically associated with riparian habitats in the desert Southwest, is largely absent from much of its former range in southern California (Sweet personal communication). In Arizona and Utah, *B. microscaphus* is known to hybridize with a closely related toad, *B. woodhousii*, and it appears that *B. woodhousii* has replaced *B. microscaphus* at a number of localities (Sullivan 1986). Given the interest in this species and the lack of information on populations in Arizona, I initiated a survey of the distribution of this toad in Arizona in 1990. Herein I present the results of this survey and compare the historic and present distributions of *Bufo microscaphus microscaphus* in Arizona.

MATERIALS AND METHODS

Historic localities were determined by examining all *Bufo microscaphus* present in the following collections (abbreviations follow Edwards 1975): ASU, CAS, CM, LACM, MVZ, UAZ, and UMMZ. Additional historic localities were determined from literature records through 1988 (Price and Sullivan 1988). Historic localities (Fig. 1) throughout the state were surveyed to a limited degree in 1990 and more intensively in 1991 and 1992 (each site was visited on 1–8 occasions). All sites were photographed and searched for toads and larvae during the late winter and spring (February through June). If juvenile or adult toads were found, they were measured (snout-vent length in mm, SVL), photographed, and released or retained as voucher specimens (deposited in the ASU Vertebrate Collection). If larvae were present, a sample was collected and returned to the laboratory for rearing to allow confident identification (larvae of *Bufo woodhousii* and *B. microscaphus* are difficult to distinguish).

Adult hybrids between *B. microscaphus* and *B. woodhousii* were identified primarily on the basis of morphological variation (Sullivan 1986). *Bufo microscaphus* typically lacks (1) cranial crests, (2) a well-defined dorsal stripe, and (3) dark ventral pigmentation. In addition, given species-specific differences in vocalizations, advertisement calls were recorded in the field and release calls were recorded under laboratory conditions for breeding males. Cloacal temperatures were recorded with a Weber Quick-recording thermometer to allow assessment of temperature effects on vocalizations (Sullivan 1992). Calls were analyzed subsequently following the methods outlined in Sullivan (1992).

RESULTS

North of the Grand Canyon, *B. microscaphus* has been recorded from the Virgin River at Littlefield and from Beaver Dam Wash near its confluence with the Virgin River at Littlefield (Fig. 1). *Bufo microscaphus* has also been recorded from Short Creek near Colorado City (route 389). In 1991 and 1992 *B. microscaphus* were taken at Beaver Dam Wash, 2 km northeast of Littlefield, and in the Virgin River Gorge, 20 km northeast of Littlefield (Fig. 1). *Bufo woodhousii* and hybrids

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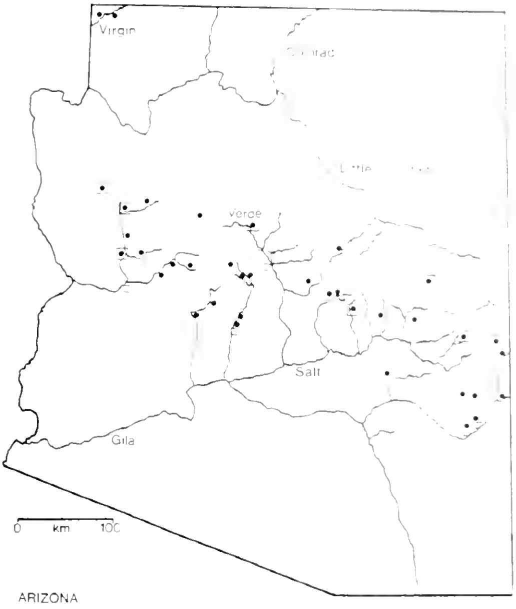

Fig. 1. Historic and recent collecting localities for *Bufo microscaphus* in Arizona. Major drainages are labeled. Solid circles (●) represent sites where *B. microscaphus* was observed during 1991–92; solid circles enclosed by squares (⊡) represent historic localities (<1990) that were not visited during the study, but likely continue to be occupied by *B. microscaphus* (not all historic localities are indicated). Open squares (☐) represent historic sites no longer occupied by *B. microscaphus*; *B. woodhousii* was present at most of these sites.

were also found at both sites. Suitable habitat (i.e., riparian plant growth, water) is no longer present at the Short Creek site.

In west central Arizona, *B. microscaphus* has been recorded from the Big Sandy River (Signal, Wikieup) and its tributaries (Burro Creek, vicinity of the Hualapai Mountains, Trout Creek); the Santa Maria River (route 93 crossing) and its tributaries (Kirkland Creek); and the Bill Williams proper (Alamo Crossing, 1950; Fig. 1). In 1991 *B. microscaphus* was observed and/or taken on the Big Sandy (route 93 crossing), Burro Creek (route 93 crossing), Santa Maria River (crossings at routes 93 and 96), and Kirkland Creek (route 96 crossing; Fig. 1). Breeding aggregations at Burro Creek ($N = 15$ calling males, $N = 3$ ovipositing females) and the Santa Maria River ($N = 10$ calling males estimated at route 93 crossing) on 22 February 1991 indicate thriving populations. Numerous apparently pure *B. woodhousii* were taken or heard calling at Alamo Lake on 12 July 1991; no *B. microscaphus* were observed.

Bufo microscaphus has been recorded from the Hassayampa River at a number of sites: immediately south of Wickenburg, at the Rincon Road crossing (5 km north of Wickenburg), at the box canyon approximately 5 km northwest of Wickenburg, and near Wagoner (Fig. 1). In 1990–92 *B. microscaphus* was observed along the Hassayampa River approximately 5 km southeast of Wickenburg (Fig. 1). Numbers of breeding adults (12–15 males and 3–5 females over a 200-m section of the river during 1990 and 1991) suggest a thriving population. Although *B. woodhousii* was recorded from this site in 1985–86 ($N = 6$ total), on the basis of morphology and vocalizations, none (or possible hybrids) has been noted since 1986. A few adult *B. microscaphus* ($N = 3$) were observed at Wagoner along the upper Hassayampa in 1990.

Bufo microscaphus have been taken along the Agua Fria River (mouth of Boulder Creek, Rock Springs), upper Turkey Creek (Battle Flat south of Mayer), and Cave Creek (2 km north of Cave Creek; Fig. 1). Although Sullivan (1986) found both southwestern and Woodhouse's toads and their hybrids at the Agua Fria River near the mouth of Boulder Creek (Table Mesa road crossing) in 1984, since that time only a single *Bufo microscaphus* has been taken (in 1992); all other individuals have been *B. woodhousii*-like (Fig. 1). Large breeding aggregations ($N = 10–50$ individuals) of apparently pure *B. microscaphus* were observed in the spring of 1992 along the Agua Fria River 1 km northeast of Black Canyon City.

Bufo microscaphus have been taken from Granite Creek (just north of Prescott), Oak Creek (Sedona), Webber Creek (10 km east of Pine), and the Verde River proper (at Perkinsville and the Verde Valley at mouth of Wet Beaver Creek; Fig. 1). A single adult *B. microscaphus* was observed along Webber Creek (10 km east of Pine) in 1990. A single toad was observed on the Simmons–Camp Wood road northwest of Prescott during the spring of 1991 (Howland personal communication). A breeding aggregation of *B. microscaphus* ($N = 12$ males) was observed at Granite Creek (just east of the route 89 crossing, 2 km northeast of Prescott) on 7 May

TABLE [illegible]. Localities where *Bufo microscaphus* was present in 1991–92: T = township, R = range, S = section.

No.	County	Locality data (T, R, S)
1	Coconino	East Clear Creek at Jones Crossing (T13N, R10E, S10)
2	Gila	Cedar Creek at rte 73 crossing (T, R, and S unavailable)
3	Gila	Tonto Creek at rte 260 crossing (T11N, R12E, S21)
4	Gila	Creek north of San Carlos on road to Sawmill (T, R, and S unavailable)
5	Graham	Bonita Creek north of confluence with Gila River (T6S, R28E, S16)
6	Greenlee	Upper Eagle Creek northwest of rte 666 on road to Honeymoon (T1S, R28E, S20)
7	Greenlee	Blue River southeast of rte 666, near town of Blue (T3N, R31E, S22)
8	Maricopa	Hassayampa River, southeast of Wickenburg (T7N, R4W, S20)
9	Mohave	Beaver Dam Wash (T40N, R15W, S5)
10	Mohave	Big Sandy Wash at rte 93 crossing (T15N, R13W, S1)
11	Mohave	Burro Creek at rte 93 crossing (T14N, R11W, S19)
12	Mohave	Virgin River, Virgin River Gorge Campground (T41N, R14W, S15)
13	Yavapai	Agua Fria River, Black Canyon City (T9N, R2E, S35)
14	Yavapai	Agua Fria River at Table Mesa Road crossing (T7N, R2E, S6)
15	Yavapai	Agua Fria River at rte 169 crossing (T13N, R1E, S2)
16	Yavapai	Big Bug Creek, vicinity of Mayer (T12N, R1E, S28)
17	Yavapai	Black Canyon Creek, north of Black Canyon City (T9N, R2E, S28)
18	Yavapai	Granite Creek, northeast of Prescott (T14N, R2W, S26)
19	Yavapai	Hassayampa River, vicinity of Wagoner (T10N, R3W, S14)
20	Yavapai	Kirkland Creek at rte 96 crossing (T13N, R6W, S9)
21	Yavapai	Santa Maria River at rte 93 crossing (T12N, R9W, S15)
22	Yavapai	Santa Maria River at rte 96 crossing (T13N, R8W, S17)

1991; larvae and adults were found near Mayer and Dewey, respectively, in 1992. *Bufo woodhousii* occurs sympatrically with *B. microscaphus* in the vicinity of Prescott and Dewey, and there is evidence of hybridization near the latter site.

No *B. microscaphus* were observed at a number of points along the Verde River: near Paulden (1 visit in 1991), approximately 3 km north of Clarkdale (1 visit in 1991), at the mouths of Wet Beaver and West Clear creeks (total of 3 visits in 1990–91), or along the East Verde River at the route 87 crossing and 10 km east of the route 87 crossing (3 visits in 1990–91). Similarly, no *B. microscaphus* were apparent along Oak Creek (south of Sedona) on three visits in 1990–91. Habitats at most of these locations (e.g., lentic aquatic sites) may favor *B. woodhousii*, which has been recorded from the Verde Valley since at least the 1950s. A number of larvae and/or adult *B. woodhousii* were taken at the Verde River (3 km north of Clarkdale), along Oak Creek (near Cornville), and along Wet Beaver Creek (in the vicinity of Lake Montezuma) in 1990 and 1991.

Bufo microscaphus have been taken along East Clear Creek (Jones Crossing) and Silver Creek (5 km south of Show Low) from the late 1970s through the mid-1980s (Fig. 1). Juvenile *B. microscaphus* were observed immediately downstream from the Blue Ridge Reservoir on East Clear Creek in May of 1990; larvae were abundant at Jones Crossing of East Clear Creek on 17 July 1991.

In central and east central Arizona, *B. m. microscaphus* have been taken near Tonto Creek (route 260), Cherry Creek (vicinity of Young), near Sawmill (Sawmill Canyon, 17 km east of route 77), the vicinity of Point of Pines (12 km north of the Black River), and the vicinity of Maverick (near Pacheta Creek; Fig. 1). One adult *B. microscaphus* was taken at the route 260 crossing of Tonto Creek (17 July 1991). Two recently metamorphosed juveniles (<25 mm SVL) were observed at Dove tank, near Cottonwood Creek, southwest of Show Low (route 60), on 12 August 1991. Larvae of *B. microscaphus* (verified by lab rearing) were abundant at Cedar Creek (route 73 crossing) on 1 July 1991, and approximately 13 km north of San Carlos (route 170) on 26 July 1991.

Bufo microscaphus have been taken from Eagle Creek (13 km west of Clifton), the San Francisco River (northeast of Clifton), and the Blue River (southeast of Alpine; Fig. 1). Larvae of *B. microscaphus* (verified by lab rearing) were abundant on Eagle Creek, 40 miles northwest of Clifton, on 12 June 1991, and on the Blue River, southeast of Alpine, on 2 July 1991.

TABLE 2. Localities where *Bufo microscaphus* was detected in 1990–92. [illegible]

Site	County	Locality data (T, R, S)
1	Gila	East Fork Verde River, east rte 87 (T, R, and S [illegible])
2	Gila	Sycamore Creek near Sunflower (T6N, R9E, S[illegible])
3	Gila	Reynolds Creek at rte 288 crossing (T6N, R13E, S18)
4	Graham	Gila River southwest of mouth of Bonita Creek (T6S, R28E, S2)
5	La Paz	Alamo Reservoir, Bill Williams River (T10N, R13W, S2)
6	Maricopa	Cave Creek (T6N, R4E, S9)
7	Mohave	Short Creek at rte 389 crossing, Colorado City (T42N, R6W, S[illegible])
8	Yavapai	Agua Fria River, south of Black Canyon City (T8N, R2E, S[illegible])
9	Yavapai	Verde River, northwest of Clarkdale (T16N, R2E, S[illegible])
10	Yavapai	West Clear Creek (T13N, R5E, S13)
11	Yavapai	Wet Beaver Creek at Lake Montezuma (T14N, R5E, S1)
12	Yavapai	Beaver Creek near confluence with Verde River (T14N, R[illegible]E, S[illegible])
13	Yavapai	Oak Creek in vicinity of Cornville (T16N, R4E, S26)

DISCUSSION

Populations of *B. microscaphus* in west central Arizona appear to be thriving. However, it is critical to note that demographic data allowing an adequate evaluation of the status of these (or any other) populations are unavailable. During 1990–91, adults, juveniles, and larvae were noted at most of the historic localities (Bill Williams and Hassayampa drainages). Over most of this area there is no immediate threat from hybridization with *B. woodhousii*. However, documentation of *B. woodhousii* at Alamo Lake suggests that areas of hybridization immediately upstream and downstream from the impoundment may have been initiated recently following establishment of lentic habitats preferred for breeding by *B. woodhousii* (Sullivan 1986). It is difficult to predict the outcome of such interactions, but in the absence of further modification of the riparian corridor it is reasonable to anticipate that *B. woodhousii* will remain confined to the general vicinity of Alamo Lake. It should be noted that in contrast to the report of Jones (1981), no *B. woodhousii* were found in 1990–92 on any of the tributaries of the Bill Williams River. Although most of the sites visited were relatively disturbed (human recreational activity, cattle and burro grazing), other than at Alamo Lake, lotic habitats preferred by *B. microscaphus* for breeding predominated.

With respect to the south central portion of the state, *B. microscaphus* is apparently no longer present on the lower reaches of the Agua Fria River or Cave Creek. Along the Agua Fria River, it appears that *B. woodhousii* has replaced *B. microscaphus* to a point just upstream from Lake Pleasant proper (Table Mesa road crossing). With the documentation of vigorous reproductive activity by *B. microscaphus* at Black Canyon City in 1992, it seems reasonable to conclude that without additional habitat alteration, *B. woodhousii* will be unable to move further upstream from the Table Mesa Road site. The expansion of Waddell Dam should provide an excellent opportunity for testing this hypothesis.

The Verde River Valley (Clarkdale to Camp Verde) is one area in which historic collections (all prior to 1960) documented *Bufo microscaphus*, but where only *B. woodhousii* are present today. The increase in lentic habitats associated with agricultural activities in the Verde Valley presumably has favored the establishment of populations of *B. woodhousii*. It is reasonable to conclude that pure populations of *B. microscaphus* remain intact along the relatively undisturbed and inaccessible sections of the Verde River (e.g., Perkinsville) and its tributaries (e.g., Sycamore Creek). For example, a "pure" breeding aggregation of *B. microscaphus* was observed at Perkinsville on the Verde River on 22 May 1989. However, the extent to which *B. woodhousii* has gained access to the major tributaries of the Verde (e.g., Wet Beaver Creek, West Clear Creek, Oak Creek) remains unclear. *B. woodhousii* is currently present on the lower reaches of all of these streams.

The abundance of [illegible] at Cave [illegible] and Bonita creeks [illegible] indicates that populations of *B.* [illegible] occur throughout [illegible] the [illegible] part of the state, but [illegible] the Gila River [illegible] hybridize with *B.* [illegible] mouths of both Bonita and Eagle creeks (Sullivan 1986, Minckley personal communication). The present results suggest that *B. woodhousii* has not moved further upstream into the tributaries of the Gila River, but additional study will be necessary to adequately assess the extent of hybridization in this region.

In summary, *B. microscaphus* is present at a number of historic localities, but absent from those where the riparian corridor has been altered dramatically through the construction of impoundments. Unfortunately, only anecdotal data are available on the status of extant populations. Additional study will be necessary to adequately assess population dynamics of this toad across its present distribution.

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DOUBLE MOUND OF THE HARVESTER ANT *POGONOMYRMEX OCCIDENTALIS* (HYMENOPTERA: FORMICIDAE, MYRMICINAE)

William H. Clark[1]

Key words: harvester ant double mound, Pogonomyrmex occidentalis, *ant nest, Utah.*

Several species of *Pogonomyrmex*, especially members of the *occidentalis* complex, have nests surmounted by a large, conical mound of soil and gravel in a clearing created by the ants (Cole 1932, 1968). I report a rare double mound of the western harvester ant, *Pogonomyrmex occidentalis* (Cresson), having two distinct mounds not joined at the bases within a single clearing (Fig. 1).

Materials and Methods

The rare double-mounded nest of *P. occidentalis* was located on 15 July 1987 in Grand County, Utah, approximately 58 km NE Moab along Highway 128 and about 1 km from the Colorado River, at an elevation of 1415 m. Voucher specimens from both mounds (WHC #8184 and 8185) are deposited in the Orma J. Smith Museum of Natural History, Albertson College of Idaho, Caldwell (CIDA).

Results and Discussion

The *P. occidentalis* nest was located in a disturbed area 5 m from the edge of Highway 128 in a clearing surrounded entirely by cheatgrass (*Bromus tectorum* [L.]). The clearing

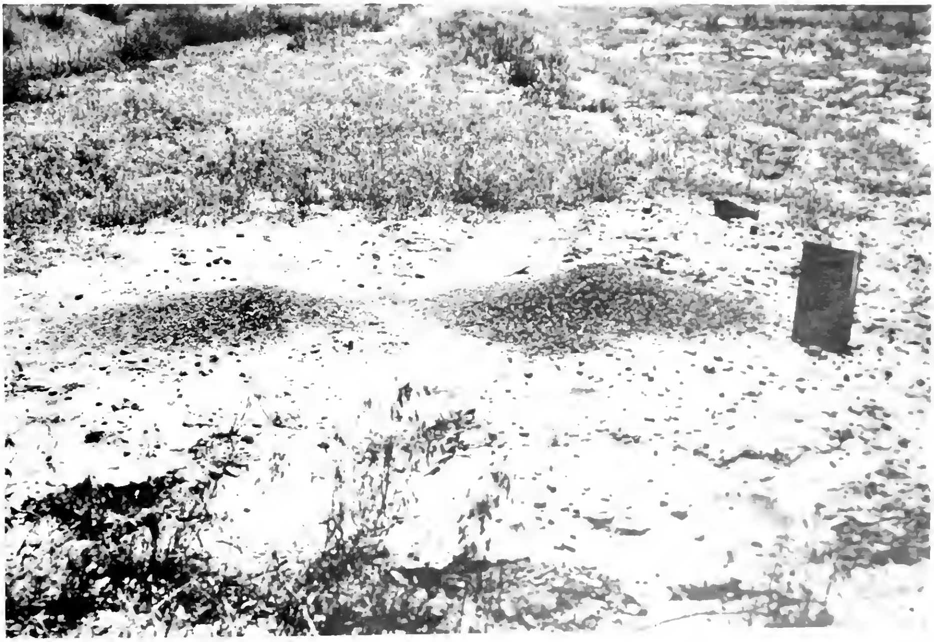

Fig. 1. Nest of *Pogonomyrmex occidentalis* (Cresson), with two mounds, in Grand County, Utah. Field book is 11 × 19 cm.

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[1] Orma J. Smith Museum of Natural History, Albertson College of Idaho, Caldwell, [illegible]

was 2.6 × 2.9 m, with one mound 50 × 50 cm in diameter and 8 cm tall, and the other 60 × 63 cm in diameter and 12 cm tall. Big sagebrush (*Artemisia tridentata* Nutt.) and greasewood (*Sarcobatus vermiculatus* [Hook.] Torr.) were the dominant shrubs in the adjacent area. The mounds were totally covered by fine gravel and scattered leaves of *S. vermiculatus*. Both mounds had east-facing entrances at their bases. Ant activity outside the nest had apparently ceased during the hot afternoon, so worker ants were collected from each mound by excavation. The shorter mound contained workers, callow workers, and brood at a depth of 5 cm; the other mound contained only workers (maximum excavation below each mound was 60 cm). The ants were placed in a field observation arena and showed no aggression toward each other, indicating that they are nestmates. Ants of the same colony can recognize each other (Sudd and Franks 1987).

Lavigne (1969) found only one queen per nest ($n = 27$) in this species. I was unable to locate a queen or queens to help resolve the question: Is this one or two nests? Queens in this species are often found deep, up to 185 cm (Lavigne 1969).

The cause of the double mound is unknown. Human disturbance is certainly a possible cause since the nest is located along a highway.

During 25 years of field observation I have not previously encountered the double-mound situation. Cole (1932) stated that for a closely related species, which is now known as *P. salinus* Olsen (Shattuck 1987), "there are many double mounds and occasionally a triple one"; no further details were given. Allred (1982) stated that in examination of 219 mounds of *P. occidentalis* in Utah, 213 were typical single mounds, while only 5 had two and 1 had three main mounds joined aboveground and apparently inhabited by the same colony. However, the six ant mounds reported by Allred (1982) shared common bases with their double/triple, which differentiates them from the nest described here (Fig. 1).

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AUTUMN-WINTER HABITAT USE OF LESSER PRAIRIE-CHICKENS (*TYMPANUCHUS PALLIDICINCTUS*, TETRAONIDAE)

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Key words: Tympanuchus pallidicinctus, *Lesser Prairie-Chicken, feeding, habitat, [illegible], New Mexico, [illegible]ing, shinnery oak.*

Knowledge of habitat use is necessary for sound management of Lesser Prairie-Chickens. Further, autumn and winter is a critical time because habitat must support prairie-chickens until the next breeding season. Studies in Colorado (Hoffman 1963), Oklahoma (Jones 1963), and Texas (Taylor and Guthery 1980) documented general vegetation types occupied by the species in autumn and winter but provided no specific data on landscape features used by Lesser Prairie-Chickens within these generalized habitats. The purpose of our study was to provide a description of vegetative characteristics at autumn and winter foraging and roosting sites of Lesser Prairie-Chickens in shinnery oak (*Quercus havardii*) grasslands in southeastern New Mexico.

STUDY AREA

The study area is approximately 15,500 ha of Bureau of Land Management lands in Chaves County, southeastern New Mexico. Topography is gently undulating to dunelike, and climate is semiarid with distinct seasons, wide ranges of diurnal and annual temperatures, and moderately low rainfall (Maker et al. 1971). The area is in the Southern Mixed Prairie Type, where the High Plains Bluestem Subtype grades westward into the Desert Prairie Subtype (Holechek et al. 1989:79, Riley et al. 1992).

MATERIALS AND METHODS

We captured eight male Lesser Prairie-Chickens on autumn leks in 1977 with cannon nets and rocket nets (Smith 1979, Davis et al. 1980). All eight males were radio-tagged and located weekly using a portable receiver and hand-held antenna (Smith 1979, Riley et al. 1992). We also located prairie-chickens by horseback with north-south transects (11 km) established at 0.8-km intervals across the study area (Jan–Feb 1978).

Use sites were identified by numerous tracks and droppings, signs of pecking and scratching, and remains of partly eaten plant material. If sign of more than one bird was present at a site, the sign of a single bird was identified by tracks in the sandy soil. No more than one use site per flock per day was identified and used. We assumed both males and females were present at use sites. At each foraging site we sampled vegetation within 50 m with a 4-arm steppoint transect because foraging did not take place at a specific spot but over a general area (Evans and Love 1957). We used an 8-arm transect at roosting sites because sites were small in size and we believed a 3-m-radius circle would adequately describe the vegetation surrounding the site (Heady et al. 1959).

RESULTS

Prairie-chicken use of the Desert Prairie Subtype was low (0/185 horseback locations and 8/161 radio locations) [illegible] use of the High Plains Bluestem Subtype. Autumn and winter foraging sites were dominated by grasses but included a moderate [illegible] shinnery oak (Table 1). Autumn foraging sites were more grassy and had [illegible] winter sites. [illegible]

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TABLE 1. Mean percent basal composition (SD) of vegetation at autumn and winter foraging and roosting sites of Lesser Prairie-Chickens, Chaves County, New Mexico, 1976–78.

	Foraging		
Species	Autumn ($n = 22$)	Winter ($n = 50$)	Roosting ($n = 20$)
GRASSES			
Andropogon hallii	7 (5.9)	7 (7.2)	16 (15.0)
A. scoparius	8 (2.4)	9 (2.5)	8 (2.5)
Sporobolus spp.	10 (3.5)	9 (1.0)	9 (2.3)
Aristida spp.	23 (3.9)	19 (8.1)	16 (9.2)
Bouteloua hirsuta	8 (1.2)	6 (1.6)	9 (2.7)
Panicum hallii	6 (2.6)	5 (1.3)	7 (4.5)
Others[a]	2	3	1
Total	63 (8.7)	59 (5.0)	66 (6.4)
SHRUBS			
Quercus havardii	32 (10.4)	38 (5.2)	32 (6.1)
Others[a]	5	3	2
Total	37 (9.3)	41 (5.3)	34 (6.4)

[a] <0.5% of total composition.

from combined autumn and winter roosting sites with those from foraging sites indicated considerable similarity in vegetation. Both foraging and roosting sites showed a dominance of grasses and substantial lesser amounts of shinnery oak. Roosting sites had more grass and less shrub than winter foraging sites. Three-awn grass composition was higher at foraging sites than at roosting sites.

DISCUSSION

Prairie-chickens were found almost entirely in the High Plains Bluestem Subtype in autumn and winter; this preference is similar to that of Lesser Prairie-Chickens in Texas (Taylor and Guthery 1980). Although the sample was small, it appears there was more shinnery oak at foraging sites in winter than in autumn. This change might suggest increased feeding on acorns in winter. The inconsistency of autumn-to-winter changes in composition of grasses might suggest changes were not directly related to prairie-chicken foraging. Changes from autumn to winter in grass composition might have been an artifact of changes in shinnery oak composition. Since percent composition always totals 100%, the increase in one species must be offset by a decrease in one or more other species.

The similarity in vegetation between roosting and foraging sites suggests that prairie-chickens might [illegible] and roosted near their foraging areas; this is in agreement with field observations. Taylor and Guthery (1980) found that mean distances between autumn and winter daily use sites of male prairie-chickens in Texas ranged from 390 to 697 m, but they found that greater distances between use sites were influenced by availability of agricultural crops. More grassy sites were apparently sought for roosting than for foraging. Selection of grassy sites for roosting was expected, considering the need for concealment and the coloration of prairie-chickens. Abundant plants, which grow large enough to provide appreciable concealment cover at roosting sites, include sand bluestem (*Andropogon hallii*), little bluestem (*Schizachyrium scoparium*), drop-seed (*Sporobolus* spp.), three-awn (*Aristida* spp.), hairy grama (*Bouteloua hirsuta*), and shinnery oak.

CONCLUSIONS

Lesser Prairie-Chickens exist in the shrub-dominated High Plains Bluestem Subtype in southeastern New Mexico by using mixed stands of tall grass and shinnery oak. To improve Lesser Prairie-Chicken autumn and winter habitat, we recommend that shinnery oak–tallgrass plant communities be managed by increasing the interspersion of tallgrass and shrub cover types. Lesser Prairie-Chicken foraging habitat can be maintained in semiarid grassland ranges where brush encroachment is not a problem with 25–35% livestock utilization of the annual growth of key forage species (Donart et al. 1978, Holechek et al. 1989). With this recommended use, rangelands of appreciable size will not be grazed uniformly. Some areas around watering points, salt grounds, valley bottoms, and trails will be heavily grazed. Remote pastures away from water, on steep slopes, or with poor accessibility due to physical barriers should receive light grazing pressure.

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